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INTEGRATIVE TAXONOMIC REVISION OF THE *Bronchocela cristatella* (KUHLE, 1820) (SQUAMATA: AGAMIDAE) SPECIES COMPLEX ACROSS THE INDONESIAN ARCHIPELAGO WITH DESIGNATIONS OF ESSENTIAL NAME-BEARING TYPES

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A.A. Thasun Amarasinghe^{1*}, Daniel Jablonski², Nikolay A. Poyarkov^{3,4},
Patrick D. Campbell⁵, Ivan Ineich⁶, Awal Riyanto¹, Alexey V. Trofimets³, Noviar Andayani⁷,
A. Abinawanto⁷, Jatna Supriatna⁷, Amir Hamidy¹ & Jakob Hallermann⁸

¹ Research Center for Biosystematics & Evolution, National Research & Innovation Agency (BRIN; Government of Indonesia), Cibinong 16911, Indonesia

² Department of Zoology, Comenius University in Bratislava, Ilkovičova 6, Mlynská dolina, 842 15 Bratislava, Slovakia; Herpetological Collection, 1st Zoological Department, Natural History Museum Vienna, Austria

³ Department of Vertebrate Zoology, Biological Faculty, Lomonosov Moscow State University, Moscow, Russia

⁴ Joint Vietnam – Russia Tropical Science & Technology Research Center, Nghia Do, Cau Giay, Hanoi, Vietnam

⁵ Department of Life Sciences, Darwin Centre, Natural History Museum, Cromwell Road, South Kensington, London SW7 5BD, England

⁶ Institut de Systématique, Évolution et Biodiversité (ISYEB), Muséum National d'Histoire Naturelle, Sorbonne Université, École Pratique des Hautes Études, Université des Antilles, CNRS, CP 30, 57 rue Cuvier, F-75005 Paris, France

⁷ Department of Biology, Faculty of Mathematics & Natural Sciences, Universitas Indonesia, Kampus UI, Depok 16424, Indonesia

⁸ Zoologisches Museum Hamburg, Leibniz-Institute for Analyses of Biodiversity Change (LIB), Martin-Luther-King-Platz 3, 20146 Hamburg, Germany

*Corresponding author. E-mail: thasun@go.brin.id

Abstract

Bronchocela cristatella (Kuhl, 1820) has been a taxonomic wastebasket due to reliance on an iconotype and an imprecise type locality. We accept Figueroa's (2021) lectotype designation and, to fix application, designate a neotype from Java (MZB 6989) that matches both the lectotype illustration and the original description. A comprehensive review of historical types and museum vouchers scored under a standardized morphometric/meristic regime, together with a 16S rRNA phylogeny sampling ten named species (six newly sequenced here), reveals three Indonesian lineages previously treated as *B. cristatella* sensu lato. Nomenclatural actions stabilize usage: we designate a lectotype for *Calotes octospinosus* (NMBE 10118463) and a neotype for *Agama moluccana* (NHMUK 1910.4.26.21),

resurrecting them as *B. octospinosa* (North Sumatra–Peninsular Malaysia and parts of West Borneo), and *B. moluccana* (Buru and adjacent central Maluku), and we resurrect *B. petersidoriai* (SE Sulawesi). Molecular analyses (mitochondrial 16S) led to the recovery of three well-supported clades consistent with species-level divergences (e.g., 6.0–6.5% *cristatella* vs. *burmana*; 3.8–4.0% *octospinosa* vs. *hayeki*; 4.8–5.0% cf. *moluccana* vs. *celebensis*), although deeper relationships remain weakly supported. Halmahera populations are treated as *B. cf. moluccana* pending multilocus tests.

Keywords: *Agama*, *Calotes*, phylogeny, Sundaland, systematics, taxonomy, Wallacea.

Introduction

The agamid genus *Bronchocela* Kaup, 1827 comprises 15 currently recognized species distributed from southern Indochina eastward through Sundaland, Wallacea, the Philippines, and into New Guinea (de Rooij 1915, Wermuth 1967, Diong & Lim 1998, Hallermann 2005, Manthey 2008, Grismer *et al.* 2015, 2016, Zug *et al.* 2017, Amarasinghe *et al.* 2022a,b, 2024, Chandramouli *et al.* 2023). Kaup (1827) established *Bronchocela* as a subgenus of *Calotes*, including *Agama gutturosa* Merrem, 1819 and *A. cristatella* Kuhl, 1820, without designating a type species. Both early descriptions referenced a single Seba (1734) specimen, but recent re-evaluation shows that Merrem's *A. gutturosa* corresponds to *B. jubata* Duméril & Bibron, 1837 (Denzler & Tillack 2024). To stabilize nomenclature, these authors treated *gutturosa* as a *nomen oblitum*, allowing the long-established name *B. jubata* to stand.

The identity of *Agama cristatella* has remained problematic for over 200 years. Kuhl (1820) cited material “in the Paris Museum” (MNHN) but did not specify the number or origin of specimens. Two historical specimens collected by Leschenault in Java between 1803 and 1807 (MNHN 6885 and MNHN 1999.8146) were almost certainly available to Kuhl before he departed for Java in 1820 and must be considered part of the original type series (Duméril & Bibron 1837, Lescure & Marty 2000, Amarasinghe *et al.* 2009, Adler 2007, 2012; Jangoux 2004, 2024). These syntypes were overlooked by Figueroa (2021), who instead designated Seba's (1734) poorly detailed illustration as the lectotype. While this action satisfies the International Code of Zoological Nomenclature (ICZN 1999), it leaves *cristatella* anchored to an iconotype lacking diagnostic value and detached from a known population. Because the historical syntypes cannot be unambiguously enumerated and the lectotype figure is inadequate for modern taxonomy, a neotype is required to fix the application of *B. cristatella* in accordance with ICZN Article 75.

Across its broad geographic scope, *B. cristatella* sensu lato has long been considered problematic because it exhibits deep phylogenetic divergence and pronounced geographic morphological variation (Grismer *et al.* 2015, 2016). Several names historically subsumed within *cristatella* have been resurrected or re-evaluated, including *B. burmana* Blanford, 1878 from Myanmar (Zug *et al.* 2017), *Agama moluccana* Lesson, 1830 from Buru Island, *Calotes octospinosus* Baumann, 1913 from northern Sumatra, and *B. petersidoriai* Böhme & Bischoff, 1984 from southeastern Sulawesi. Other names, such as Fitzinger's (1861) *Pseudocalotes archiducissae*, were later designated *nomina nuda* (Das & Gemel 2000). Philippine populations form a deeply divergent lineage (20–30% uncorrected ND2 distance) relative to Indonesian *Bronchocela* but not conspecific with Indonesian *B. cristatella*. (Grismer *et al.* 2015). Philippine material has been associated with both *Bronchocela marmorata* Gray, 1845 (type locality: ‘Philippine Islands’) and *Calotes philippinus* Peters, 1867. Because the present revision focuses on Indonesian populations, we treat Philippine specimens only for comparative context and exclude them from our morphometric and phylogenetic analyses pending a dedicated revision of Philippine *Bronchocela*, which may include multiple species given the archipelago's distinct faunal regions.

Despite extensive literature, the systematics of Indonesian *Bronchocela* remain unsettled for three principal reasons. First, reliance on Seba's lectotype and an imprecise type locality has obscured the identity of *B. cristatella* sensu stricto. Second, inconsistent treatment of historical synonyms, particularly *A. moluccana*, *C. octospinosus*, and *B. petersidoriai*, has led to unstable taxonomy across museum collections and field guides. Third, although morphological variation is widely noted, most quantitative studies have focused on Peninsular Malaysian and Philippine lineages (Grismer *et al.* 2015,

2016), leaving Indonesian diversity under-sampled and only partially resolved. Molecular work has similarly been fragmentary: ND2 sequences from earlier studies revealed deep divergence among Peninsular Malaysian and Philippine lineages, but Indonesian populations remain poorly represented in phylogenetic analyses.

To address these problems, we conducted an integrative taxonomic revision of the *B. cristatella* complex across the Indonesian Archipelago. We examined the full historical series, redescribed type-relevant material, and re-evaluated nomenclatural hypotheses under ICZN criteria. A neotype is designated for *A. cristatella* from Java, stabilizing the name *B. cristatella* sensu stricto. We further examined museum specimens using standardized meristic and morphometric protocols and generated a mitochondrial (16S rRNA) phylogeny sampling 10 species of *Bronchocela*, including newly sequenced Indonesian material. Our goals were: (1) to clarify the identity and diagnostic boundaries of *B. cristatella* sensu stricto; (2) to evaluate the status of historically associated nominal taxa (*B. moluccana*, *B. octospinosus*, and *B. petersidorai*); (3) to reassess species-level lineages within Indonesian *Bronchocela* using integrative evidence; and (4) to revise the taxonomy, nomenclature, and type designations necessary to stabilize nomenclature across Sundaland and Wallacea.

The results reveal that *B. cristatella* sensu lato in Indonesia comprises multiple evolutionarily and morphologically distinct lineages assignable to available historical names. Our combined morphological and molecular analyses support the recognition of *B. cristatella* (Java–southern Sumatra–southern Kalimantan), *B. octospinosus* (northern Sumatra–Peninsular Malaysia–western Borneo), *B. moluccana* (Buru and adjacent central Maluku), and *B. petersidorai* (Southeast Sulawesi) as distinct species. These findings resolve long-standing ambiguities surrounding type localities, nomenclatural histories, and species boundaries within one of Indonesia's most widely distributed arboreal agamid lizards.

Materials and Methods

Specimens examined. We examined all historically relevant material associated with the *Bronchocela cristatella* complex (sensu lato), including original descriptions, historical type series, and museum vouchers spanning Java, Sumatra, Borneo, Sulawesi, Bali, Maluku, and

Papua (full list in Appendix). Our survey incorporated preserved specimens representing all nominal taxa historically linked to *B. cristatella*, including *Agama moluccana*, *Calotes octospinosus*, and *B. petersidorai*. Specimens were sourced from major international museums following Sabaj (2020) for institutional acronyms.

Fresh specimens were collected by hand and euthanized using sodium pentobarbital. Standard fixation in 10% buffered formalin for 24 h was followed by rinsing and long-term storage in 70% ethanol. Tissue samples (liver or muscle) from fresh material were preserved in 95% ethanol and stored at -20°C for molecular analysis. The neotype of *B. cristatella* (MZB 6989) possesses an associated tissue sample (voucher BSI-FS0053), although this specimen was not successfully sequenced.

Philippine material was not included in this revision because (1) it lies outside the Indonesian geographic scope of this study; (2) none of Kuhl's syntypes or the neotype originates from the Philippines; and (3) genetic data show Philippine *Bronchocela* are deeply divergent from Indonesian populations (see Grismer *et al.* 2015). Thus, Philippine lineages do not inform the application of *B. cristatella* sensu stricto or any nomenclatural action within Indonesia.

Morphological characters and measurements. Morphometric and meristic data were obtained from 642 museum vouchers (Appendix). Measurements were taken on the left side of the body for bilaterally symmetric traits using Mitutoyo digital calipers (to 0.1 mm) under stereomicroscopes (Wild M3Z, Wild M8, or Zeiss DRC). The following morphometric characters were recorded: snout–vent length (SVL, measured from tip of snout to anterior margin of vent), axilla–groin length (distance between axilla and groin), head length (distance between posterior edge of mandible and tip of snout), head width (maximum width of head), eye–nostril length (distance between anterior-most point of orbit and posterior border of nostril), snout length (distance between anterior-most point of orbit and tip of snout), orbit diameter (longitudinal largest diameter of orbit), tympanum–eye length (distance between anterior-most margin of tympanum and posterior-most margin of orbit), lower-arm length (distance from elbow to wrist with both upper arm and palm flexed), palm length [distance between wrist (carpus) and tip of longest finger, with both palm and lower arm

flexed], tibia length (distance between knee and heel, with both tibia and tarsus flexed), foot length (distance between heel and tip of longest toe, with both foot and tibia flexed), tail length (measured entire tail from posterior margin of vent to tail tip).

Meristic counts followed recent systematic treatments of *Bronhocela* (Hallermann 2005, Grismer *et al.* 2015; Amarasinghe *et al.* 2022a,b, 2024) with clarifications to eliminate ambiguity. Supralabials and infralabials were counted from the first scale contacting the rostral or mental to the last scale, distinctly larger than the surrounding granules. Canthal scales were counted between the supranasal and the anterior margin of the orbit. Temporal scales were counted in a straight line between the posterior edge of the orbit and the anterior edge of the tympanum. Paravertebrals were counted from the first crest scale behind the occiput to the last scale anterior to the vent. Midbody scale rows were counted around the body halfway between the axilla and groin.

Nuchal and dorsal crest terminology follows Harvey *et al.* (2014, 2017a,b). The “nuchal crest gap” and “dorsal crest gap” refer to the number of intervening vertebral scales between the last enlarged nuchal crest scale and the first dorsal crest scale; when these crests merge or are indistinct, the gap was scored as 0 or NA accordingly. Upper dorsal body rows were assessed as the number of rows directed upward on the dorsolateral surface at 30–60 degrees.

Body colouration was not included in the morphological analyses because *Bronhocela* species rapidly change colouration depending on behaviour, and preservation removes most chromatic features. However, rare, stable characters visible in long-preserved material, such as persistent white lateral blotches, were recorded when present, as these features have been shown to remain diagnostic for over a century. In the Species Accounts, meristic and morphometric ranges are followed by the mean $\pm$ 1 SD and sample size (n) in parentheses.

Assignment of specimens to phenotypes. Preliminary morphological surveys identified three geographically structured phenotypes within Indonesian *B. cristatella* sensu lato: Phenotype A: Java, southern Sumatra, southern Kalimantan; Phenotype B: northern Sumatra, western Borneo, Peninsular Malaysia; Phenotype C: Buru, Ambon, Seram. These phenotypic clusters correspond to the three historical names associated with Indonesian populations. Only

adult specimens with unambiguous locality data and reliable taxonomic identification were included in quantitative analyses to avoid error from misidentification of museum material.

Morphometric analyses. Of the 642 museum specimens examined, only a subset was suitable for quantitative morphometric analysis. We excluded 413 specimens that lacked complete measurement series, 108 juveniles for which proportional traits are not comparable to those of adults, and 54 historical or fragile specimens unsuitable for handling. This filtering yielded a final dataset of 67 adult specimens representing the three phenotypes: phenotype A ($n = 25$), phenotype B ($n = 23$), and phenotype C ($n = 19$). Males and females were initially analysed separately to evaluate sexual dimorphism, then combined after we showed interactions between sex and phenotype were negligible. Adult morphometrics (head length, head width, eye–nostril length, snout length, SVL, tibia length, lower arm length, foot length, and palm length) were log-transformed before analysis. To remove allometric effects, we applied the Leonart *et al.* (2000) size-correction method using pooled within-sex regression slopes:

$\log X_{\text{adj}} = \log X - \beta[\log(\text{SVL}) - \log(\overline{\text{SVL}})]$, where β is the pooled within-sex slope from a regression of $\log X$ on $\log(\text{SVL})$ across phenotypes (Leonart *et al.*, 2000, Chan & Grismer, 2022), and $\overline{\text{SVL}}$ is the grand mean SVL of the dataset. Slope homogeneity among phenotypes was evaluated via the $\log(\text{SVL}) \times$ phenotype interaction; when significant, we analysed group differences by ANCOVA and compared estimated marginal means at $\overline{\text{SVL}}$.

Distributional assumptions were assessed on size-corrected variables (Q–Q plots; Brown–Forsythe tests). Group differences were tested with Welch’s one-way ANOVA followed by Games–Howell pairwise comparisons, which accommodate heteroscedasticity and unbalanced sample sizes. We report omnibus statistics, adjusted pairwise P values, and effect sizes (ω^2 for the omnibus test; Hedges’ g for pairwise contrasts), together with group medians and interquartile ranges. Potential sexual dimorphism was evaluated by fitting models with sex and sex $\times$ phenotype terms to the size-corrected variables; when both terms were negligible, sexes were combined for inference while retaining sex in the size-correction step, whereas significant interactions were analysed separately by sex.

Multivariate analyses. Principal component analyses were conducted in R v4.0.4 (R Core Team 2021) using the *princomp* function on standardized (z-transformed) size-corrected variables. Separate principal component analyses were run for pooled sexes, males-only, and females-only datasets. Biplots were used to visualize clustering patterns among phenotypes.

Molecular data and phylogenetic inference. Total genomic DNA was extracted from liver or thigh muscle biopsies of freshly collected specimens (tissues stored in 95% ethanol) and from ethanol-preserved historical museum specimens using the Qiagen DNeasy™ Tissue Kit (Valencia, CA, USA), following the manufacturer's protocols. Formalin-fixed tissues were pretreated in Gibco™ phosphate-buffered saline (pH 7.2) before DNA extraction.

For this study, we targeted a ~500 bp fragment of the mitochondrial 16S rRNA gene, amplified using primers 16Sar and 16Sbr (Palumbi *et al.* 1991; Sup. Table 1). Although earlier phylogenetic studies of *Bronchocela* have used ND2 as the primary mitochondrial marker (e.g., Mulcahy *et al.* 2018), ND2 was not sequenced here due to the age and preservation state of many specimens. Attempts to amplify ND2 and COI were made on recent historical tissues, but amplification success was extremely low, and therefore these markers were excluded. We note, however, that a broader molecular study integrating ND2 and additional loci is planned, which will allow concatenated mtDNA alignments for more comprehensive phylogenetic resolution.

PCR reactions (25 µl) contained ~10–30 ng genomic DNA, 1 µM of each primer, 0.5 µl of 20 µM dNTPs, 5 µl of 5× buffer, 1 µl of 5 mM MgCl₂, 0.25 µl of Taq DNA polymerase (5 U / µl), and ultra-pure H₂O to volume. Amplifications were performed on a SimpliAmp™ thermal cycler under the following conditions: initial denaturation at 94 °C for 5 min; 36 cycles of 94 °C for 30 s, 55 °C for 30 s, and 72 °C for 90 s; and a final extension at 72 °C for 10 min. PCR products were visualized on 0.8% agarose gels, purified, and sequenced by Macrogen Europe (Amsterdam, The Netherlands).

Newly generated sequences were deposited in GenBank (Sup. Table 2). The outgroup taxon was *Gonocephalus robinsonii*. Additional ingroup and outgroup sequences were obtained from Mulcahy *et al.* (2018) (Sup. Table 2). Sequences were aligned in MEGA v6 (Tamura *et*

al. 2013) using ClustalW (Thompson *et al.* 2003) with default parameters.

Phylogenetic analyses were conducted using both Bayesian inference and maximum likelihood. Bayesian inference analyses were performed in MrBayes v3.2.6 (Ronquist *et al.* 2012) with four Markov chains (one cold, three heated) run for 20 million generations, sampling every 5,000 generations. Convergence was assessed using the average standard deviation of split frequencies (<0.01) and parameter diagnostics in Tracer v1.5 (Rambaut & Drummond 2009), ensuring effective sample sizes > 200. The first 25% of sampled trees were discarded as burn-in, and the consensus tree with posterior probabilities was summarized from the remaining trees. Maximum likelihood analysis was performed in IQ-TREE v1.6.12 (Nguyen *et al.* 2015) using ModelFinder (Kalyaanamoorthy *et al.* 2017) to select the best-fit substitution model according to the Bayesian Information Criterion (BIC). The chosen model was HKY+F+G4, with estimated base frequencies A = 0.366, C = 0.237, G = 0.196, T = 0.201, and a gamma shape parameter (α) of 0.210 to model among-site rate heterogeneity. The final maximum-likelihood tree had a log-likelihood score of -7489.176. Branch support was assessed using 1,000 ultrafast bootstrap replicates (UFBoot; Minh *et al.* 2013, Hoang *et al.* 2018) and SH-like approximate likelihood ratio tests (SH-aLRT) with 1,000 replicates. Nodes with posterior probabilities ≥ 0.95 (Bayesian inference) and bootstrap values ≥ 70% (Maximum likelihood) were considered strongly supported, whereas values below these thresholds were treated as unsupported. Resulting trees from Bayesian inference and Maximum likelihood analyses were visualized in FigTree v1.4.2 (Rambaut 2014) and edited for presentation in Adobe Photoshop CS3.

Results

Morphometric differentiation. Morphometric analyses revealed clear phenotypic differentiation among the three recognized forms of *B. cristatella* sensu lato (namely phenotypes A, B, and C; Fig. 1A; Sup. Tables 3–5). Size-corrected comparisons identified significant among-phenotype differences in head length (head length_adj: $F_{2,39.6} = 14.72$, $p = 1.66 \times 10^{-5}$, $\omega^2 = 0.21$), eye–nostril length (eye–nostril length_adj: $F_{2,39.7} = 12.39$, $p = 6.58 \times 10^{-5}$, $\omega^2 = 0.24$), and snout length (snout length_adj: $F_{2,39.8} = 22.92$, $p = 2.39 \times 10^{-7}$, $\omega^2 = 0.32$). No other

morphometric variables showed significant differences once body size was accounted for. Post hoc Games–Howell tests indicated that phenotype C (Central Maluku) possessed

significantly greater head length, eye–nostril length, and snout length than both phenotype A (Java, southern Sumatra, southern Kalimantan) and phenotype B (northern Sumatra).

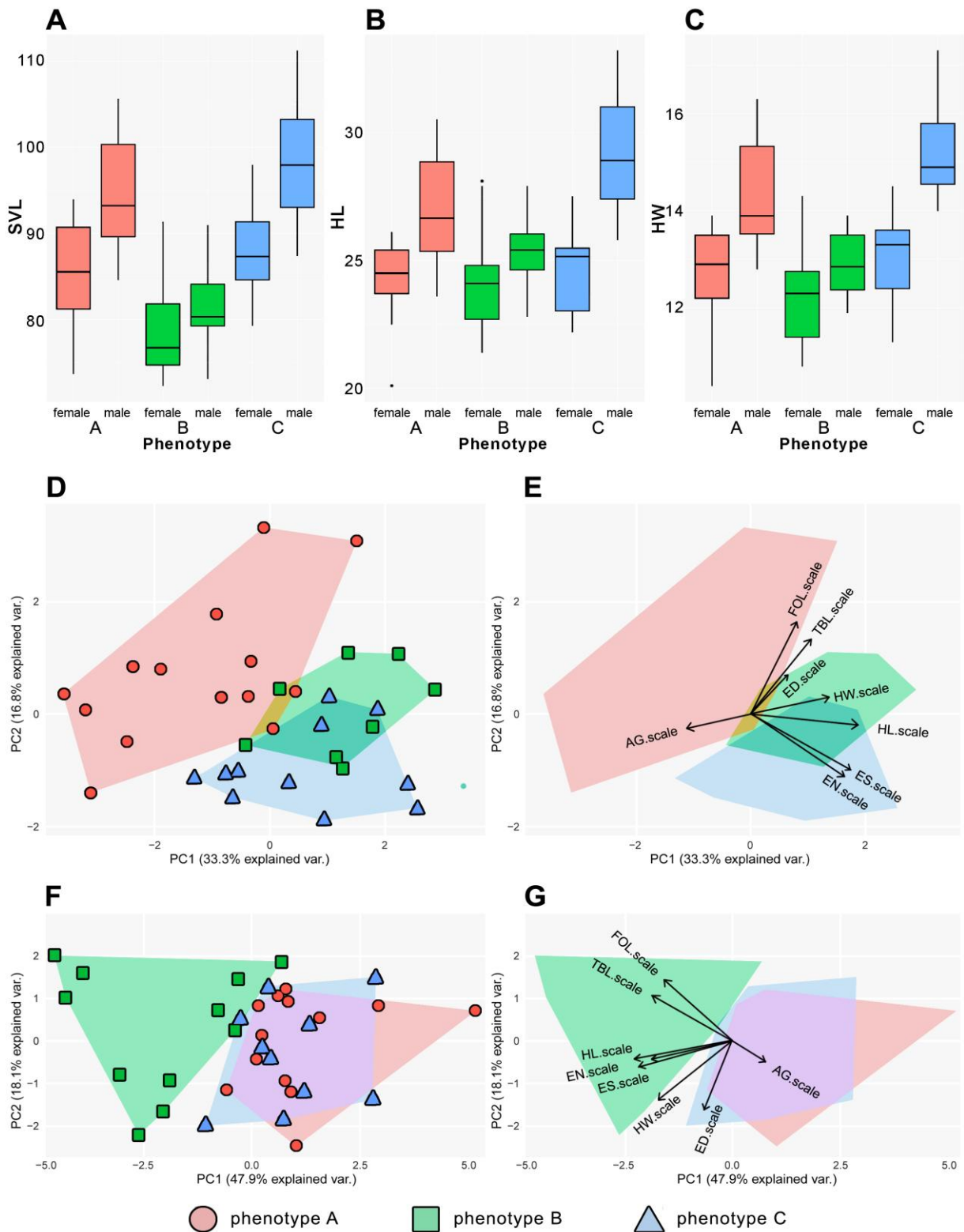


Figure 1. Boxplots of (A) snout–vent length (SVL), (B) head length, and (C) head width. Principal component analysis biplots of morphometric variation among three phenotypes of *Bronhocela cristatella* sensu lato in (D) males and (F) females. Corresponding biplots with loading vectors associated with population clusters are shown in (E) and (G), respectively. PC = principal component.

Phenotype A also exceeded phenotype B in eye–nostril length and snout length. These differences corroborate the qualitative observation that phenotype C exhibits proportionally larger heads and longer snouts.

Sexual dimorphism. Sexual dimorphism was marked in several traits (Sup. Table 6). Males had significantly greater snout length (Hedges' $g = 0.84$), head length ($g = 0.91$), and head width ($g = 0.97$) than females, all in the “large” effect category. Females, by contrast, showed longer axilla–groin distances (axilla–groin distance_adj: $g = -0.79$, “moderate” female bias), while eye–nostril length_adj displayed a small–moderate male bias ($g = 0.48$). These patterns suggest strong sexual selection on male head and snout dimensions, potentially linked to display or combat, and a corresponding relative trunk elongation in females, possibly reflecting reproductive constraints.

Principal component analysis. Principal component analysis further supported these distinctions (Fig. 1B–C; Sup. Table 7). In males, PC1 and PC2 jointly explained 50.1% of the total variance; PC1 was dominated by positive loadings for head length, head width, eye–nostril length, snout length, and limb variables (tibia length, foot length), with axilla–groin distance loading negatively, while PC2 retained positive contributions from head width, eye diameter, tibia length, and foot length. Phenotype C formed a discrete, non-overlapping cluster, whereas A and B overlapped partially. In females, PC1 and PC2 accounted for 66.0% of total variance; PC1 had negative loadings for head length, head width, eye diameter, snout length, and eye–nostril length, while PC2 was driven mainly by tibia length and foot length. Here, phenotypes A and C showed greater overlap, with phenotype B tending toward smaller head proportions. Collectively, the multivariate and univariate results confirm that phenotype C is morphometrically distinct, characterized by larger absolute and relative head dimensions, and that sexual dimorphism in head traits is both strong and directionally consistent across populations.

Comparison of type-relevant material. Morphological comparison of the two MNHN paralectotypes of *Agama cristatella* with the neotype we designated (Table 1) confirms that all three represent the same Javan phenotype. All share 10–12 lanceolate nuchal crest scales, strongly keeled lateral scales, indistinct dorsal crests, and similar relative head dimensions,

supporting the neotype's assignment to the *B. cristatella* sensu stricto lineage. Lectotype material of *Calotes octospinosus* (NMBE 10118463) conforms to our phenotype B, with crescent-shaped nuchal crest scales, 8–10 dorsolateral rows, 12–14 enlarged ventral rows, and a distinct anterior dorsal crest. The neotype designated for *Agama moluccana* (NHMUK 1910.4.26.21) represents phenotype C and matches the suite of characters observed in central Maluku populations, including feebly keeled lateral scales, a developed dorsal crest with a 4–6 scale gap posterior to the nuchal crest, and 10–14 nuchal crest scales.

Morphological delimitation of Indonesian lineages. Integration of morphometric, meristic, and qualitative characters supports recognition of three major Indonesian lineages formerly included within *B. cristatella*: (1) *B. cristatella* sensu stricto (Java–southern Sumatra–southern Kalimantan); (2) *B. octospinosa* (northern Sumatra–western Borneo–Peninsular Malaysia), and (3) *B. moluccana* (Buru–Ambon–Seram). A fourth species, *B. petersidoriai*, is morphologically distinct in possessing strongly keeled lateral scales, 12 lanceolate nuchal crest scales, and a small gular pouch, and is restricted to Southeast Sulawesi, Buton Island, and parts of Central Sulawesi.

Multivariate separation of Maluku vs. Halmahera populations. Central Maluku (*B. moluccana* sensu stricto) and Halmahera populations exhibited significant multivariate differences (MANOVA: Wilks' $\lambda = 0.235$, $p < 0.00001$; Sup. Table 8). Size-corrected pairwise tests identified consistent differentiation in eye–nostril length, snout length, tibia length, lower arm length, eye–tympanum length, and axilla–groin length (Sup. Table 9). Because no genetic material is yet available from Buru, Halmahera specimens are treated conservatively as *B. cf. moluccana* pending multilocus data.

Linear univariate tests identified six traits differing significantly between groups after size correction: eye–tympanum length ($t = 2.82$, $p = 0.0086$, Hedges' $g = 0.85$), tibia length ($t = 2.80$, $p = 0.0102$, $g = 0.94$), eye–nostril length ($t = 2.70$, $p = 0.0117$, $g = 0.85$), lower arm length ($t = 2.50$, $p = 0.0202$, $g = 0.85$), snout length ($t = 2.21$, $p = 0.0343$, $g = 0.64$), and axilla–groin length ($t = -2.11$, $p = 0.0437$, $g = -0.65$; Sup. Table 9). Effect sizes for these differences were generally moderate to large, indicating consistent divergence in head and limb dimensions, as well as trunk proportions. Given these statistically

supported morphological distinctions and the absence of genetic material from the type locality (Buru Island), hereafter we treat the Halmahera population as *B. cf. moluccana* pending broader multilocus phylogenetic analyses.

Molecular phylogeny of the Indonesian species. Our 16S rRNA maximum-likelihood and Bayesian analyses recovered three strongly supported major Indonesian clades corresponding to phenotypes A–C (Fig. 2; Sup. Fig. 1). (1) *B. cristatella* formed a clade sister to *B. burmana* from Myanmar and Thailand, with strong support (UFBoot = 95.7%, SH-aLRT = 98%). (2) *B. octospinosa* was recovered as sister to *B. hayeki*, also with strong support (UFBoot = 99.4%, SH-aLRT = 100%). (3) Specimens from the northern and central Maluku region formed a clade sister to *B. celebensis* from Sulawesi (UFBoot = 92.6%, SH-aLRT = 95%), together

with other northern Moluccan populations. All major lineages exhibited considerable genetic divergence from other *Bronhocela* taxa in mainland Sundaland and the Nicobar Archipelago. Uncorrected pairwise p-distances (Sup. Table 10) indicated that *B. cf. moluccana* differed from its sister species *B. celebensis* by 4.8–5.0%, *B. octospinosa* from *B. hayeki* by 3.8–4.0%, and *B. cristatella* from *B. burmana* by 6.0–6.5%, while differing from its sympatric congener *B. jubata* by 6.2–7.2%.

While several interspecific nodes had strong support in both Maximum likelihood and Bayesian inference analyses, some deeper nodes remained weakly supported (UFBoot < 95%; posterior < 0.95), particularly in relationships among Wallacean and Sundaland clades. These relationships will be reassessed with additional loci.

Table 1. Comparative morphology of the MNHN paralectotypes of *Agama cristatella* and the neotype designated (MZB 6989) was evaluated against the diagnostic elements of Kuhl's (1820) original description.

Character	MNHN 6885 (paralectotype)	MNHN 1999.8146 (paralectotype)	Neotype MZB 6989	Kuhl (1820)
Sex	adult male	adult male	adult male	—
SVL (mm)	85	84.6	92.6	moderate
Tail length (mm)	300	310	300	—
Head length (mm)	21.25	25.5	26.5	elongated head
Head width (mm)	11	13.1	13.6	consistent
Snout length (mm)	7.9	9.4	9.8	snout > eye
Eye diameter (mm)	6.9	8.2	8.2	—
eye diameter/snout length	0.87	0.87	0.84	—
Tympanum-eye (mm)	3.7	4.4	5.2	orbit > tympanum
Temporal scale rows	6–8	7–8	4–6	—
Temporal scales	keeled	keeled	keeled	keels on cheek
Nuchal crest shape	lanceolate	lanceolate	lanceolate	—
Nuchal crest scale count	10–12	10	12	pointed scales
Dorsal crest	absent	absent	absent	weak
Upper dorsolateral rows	4–6	7–8	7–8	—
Midbody rows	68	79	64	numerous
Ventrals (count)	70	82	63	enlarged
Enlarged ventral rows	10–12	12	12	—
Paravertebrals	105	105	103	consistent
Toe IV lamellae	32	31	36	consistent
Supralabials	10	10	10	—
Infralabials	10	11	10	within variation
Canthal scales	5	5	5	—
Canthal edge	sharp	sharp	sharp	sharp snout ridge
Superciliary scales	6	6	6	—
Post-superciliary	4	4	4	—
Midgular scales	not enlarged	not enlarged	not enlarged	—
Gular pouch	small	small	very small	slightly distended throat
Finger III vs IV	III = IV	III = IV	III = IV	—
Locality	Java	Java	Java	Java

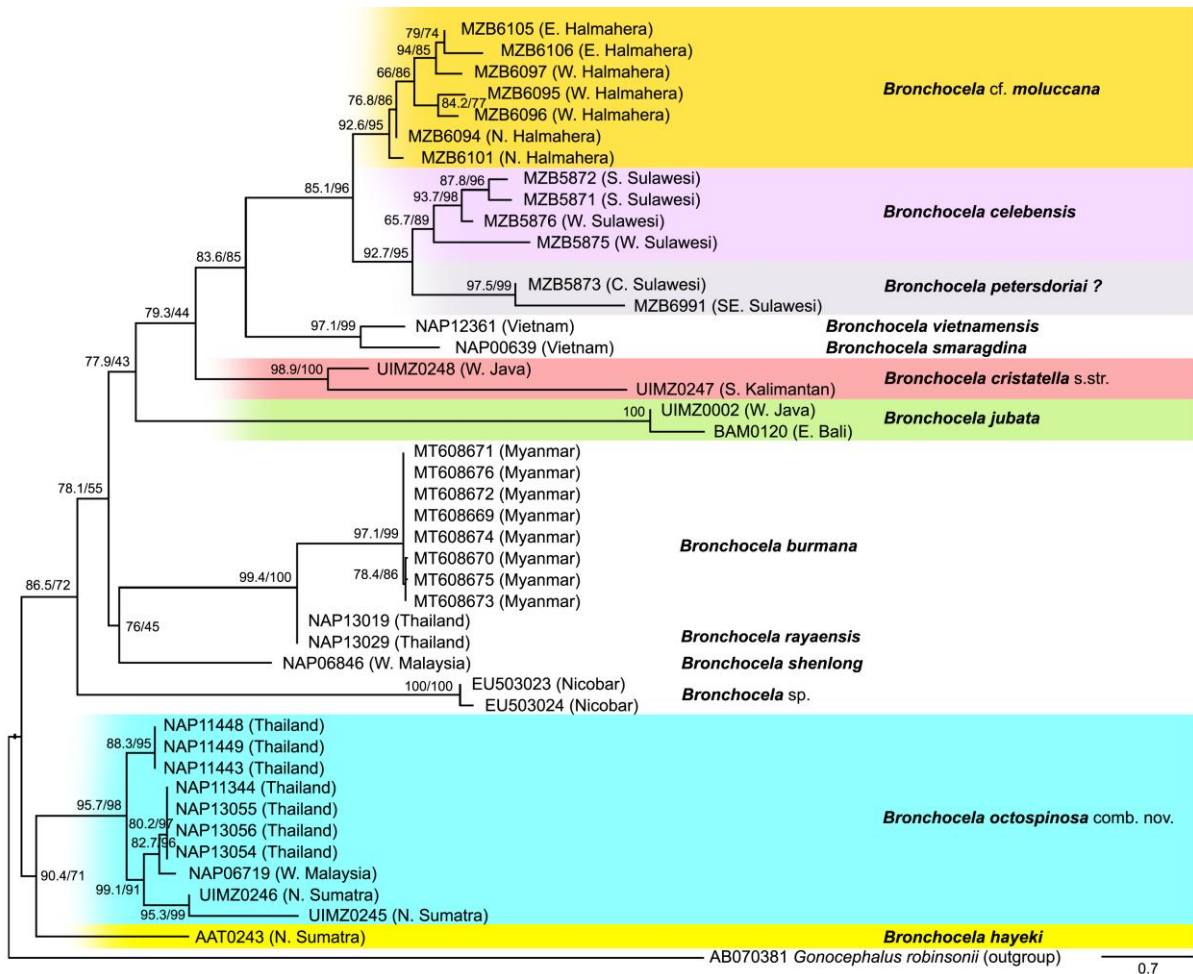


Figure 2. Maximum-likelihood phylogeny of the genus *Bronchocela* based on ~500 bp of the mitochondrial 16S rRNA gene. The topologies recovered by Maximum likelihood and Bayesian inference were congruent (see Sup. Fig. S1). A question mark next to a taxon name indicates provisional assignments in the absence of sequence data from name-bearing types or topotypic material.

Two Sulawesi samples (MZB 5873 from Central Sulawesi and MZB 6991 from Southeast Sulawesi) formed a distinct lineage sister to *B. celebensis*; we tentatively refer this lineage to *B. petersidoriai* pending sequence data from topotypic material.

Taxonomy

Taken together, our phylogeny and morphology consistently reveal three major morphological complexes within *Bronchocela*: (1) *B. jubata* complex, which includes *B. cyanopalpebra*, *B. hayeki*, *B. jubata*, *B. octospinosa*, *B. orlovi*, and *B. rubrigularis*; (2) *B. celebensis* complex, which includes *B. celebensis*, *B. marmorata* sensu stricto, *B. smaragdina*, and *B. vietnamensis*; and (3) *B. cristatella* complex, which includes *B. burmana*, *B. cristatella* sensu stricto, *B. danieli*, *B. moluccana*, *B. nicobarica*, *B. petersidoriai*, and *B. shenlong*. These complexes summarize stable combinations of meristic, morphometric,

and qualitative characters that recur across species. Members of the *B. cristatella* complex typically exhibit lanceolate nuchal crest scales, weak or indistinct dorsal crests, and narrow, strongly keeled lateral body scales. Species assigned to the *B. jubata* complex generally possess well-developed dorsal crests, enlarged midgular scales, and strongly keeled, broadly acute lateral scales. The *B. celebensis* complex is characterized by moderately developed nuchal and dorsal crests, feebly to strongly keeled lateral scales, and midbody counts that are generally lower than in the other complexes. These complexes provide a practical morphological framework for organizing species-level diversity within the genus and for interpreting patterns of character evolution. Because deeper phylogenetic relationships remain weakly supported in the present single-locus dataset, the complexes are used strictly as morphological categories rather than formal taxonomic units, and future

multilocus or genomic analyses will be required to evaluate their evolutionary cohesiveness.

Interspecific comparisons revealed a suite of morphological, morphometric, and meristic characters distinguishing the focal *Bronchocela* species from their congeners. We present diagnostic data taken for all the known *Bronchocela* species (Table 2), and an extended diagnostic character table (Table 3) for *B. cristatella* plus the three resurrected species below.

Bronchocela cristatella (Kuhl, 1820) *sensu stricto* (Tables 1–3; Figs. 3A–B, 4)

Agama cristatella Kuhl, 1820:108.

Agama gutturosa Merrem, 1819:162–168. [Not examined].

Bronchocela cristatella — Kaup 1827:619; Duméril & Bibron 1837:395; Manthey 1983:25; Manthey & Grossmann 1997:160; Cox *et al.* 1998:98; Barts & Wilms 2003:4–23; Nur-Amalina *et al.* 2017:119–129; Amarasinghe *et al.* 2022b:65–82.

Bronchocela gutturosa — Kaup 1827:619.

Calotes gutturosa — Cuvier 1829:pl. 7.

Pseudocalotes archiducissae Fitzinger, 1861:387 [nomen nudum *fide* Smith 1935].

Calotes (Bronchocele) philippinus Peters, 1867:16 [partim].

Bronchocela intermedia Peters & Doria, 1878:375.

Calotes cristatellus — Boulenger 1885:316; Flower 1899:639; de Rooij 1915:121; Taylor 1922:139; Taylor 1963:886; Smith 1935:184; Hendrickson 1966:64.

Lectotype. Seba 1734:pl. 89, fig. 1 (designated by Figueroa 2021), from “Java” (iconotype; specimen lost). Paralectotypes: MNHN 6885, MNHN 1999.8146, Java.

Neotype (designated herein). Adult male (MZB 6989) from Situ Gede (7°20' 20.95"S, 108°11' 22.29"E, datum = WGS84 in all cases; 392 m above sea level), Tasikmalaya Regency, West Java, Indonesia, collected on 25 September 2004 by R. Brown.

Diagnosis. A species of *Bronchocela*, morphologically most similar to its allopatric congener, *B. burmana* in the mainland Sundaland, but differs from all species by having medium-sized body (73.7–107.2 mm SVL; 92.3 ± 8.4 , $n = 25$) in adults; relative tail length (278.4–390.0% of SVL; 332.6 ± 28.5 , $n = 25$); a small gular pouch in males; midgular scales not enlarged; 10–12 enlarged ventral scale rows; ventrals 3–5 times larger than dorsals; 60–82 ventrals (70 ± 5 , $n = 25$); lateral body scales

narrowly acute, strongly keeled; 4–6 upper dorsal scale rows on the lateral body directed upward along the body; nuchal crest weakly developed, lanceolate in shape; 10–12 nuchal crest scales to the level of axilla; longest nuchal crest scale shorter than eye diameter; dorsal crest indistinct; some scales on temporal region enlarged; 6–8 temporal scale rows between orbit and tympanum; 5–7 canthal scales between supranasal and anterior border of orbit; canthal edge sharp; 61–80 scale rows at midbody (68.9 ± 4.6 , $n = 25$); 3rd finger equal to 4th finger; 94–116 paravertebrals (104.7 ± 6.2 , $n = 25$), first paravertebral row enlarged.

Comparison. *Bronchocela cristatella* is most likely to be confused with *B. burmana*. Unlike *B. burmana* (characters in parentheses), *B. cristatella* has a tail 278.4–390.0% of SVL (vs. 240–300%), 60–82 ventrals (vs. typically fewer than 70), sharply keeled lateral body scales (vs. weakly keeled), 4–6 upwards-directed upper dorsal scale rows (vs. none), and a weak, lanceolate nuchal crest with 10–12 crest scales (vs. 6–10). The canthal edge in *B. cristatella* is sharp (vs. blunt), and the midgular scales are not enlarged (vs. not enlarged but gular pouch smaller or absent). *Bronchocela cristatella* may also be confused with *B. octospinosa* where northern Sumatra and the Peninsular regions are involved. Unlike *B. octospinosa* (characters in parentheses), *B. cristatella* has lanceolate nuchal crest scales (vs. crescent-shaped), 10–12 crest scales (vs. 8–12 but typically larger and more prominent), strongly keeled and narrowly acute lateral scales (vs. feebly keeled and broadly acute), and fewer enlarged ventral rows (10–12 vs. 12–14). Tail proportions differ, as *B. cristatella* has 278–390% tail / SVL (vs. 330–368%). It can be sympatric with *B. jubata* in western and central parts of Java, but *B. cristatella* differs by having 4–6 upward-directed dorsolateral rows (vs. 1–2), ventrals 4–5 times larger than dorsals (vs. ventrals and dorsals more or less equal in size), and a distinctly smaller gular pouch.

Description of the neotype. An adult male, SVL 92.6 mm. Head moderately large, elongate, head length 28.6% of SVL, subtriangular in dorsal and ventral aspects, head width 51.3% of head length; distinct from neck; snout elongate, snout length slightly greater than eye diameter, eye diameter 83.7% of snout length; interorbital distance broad; eye large, pupil rounded; eye diameter greater than eye-tympanum distance

Plate 18

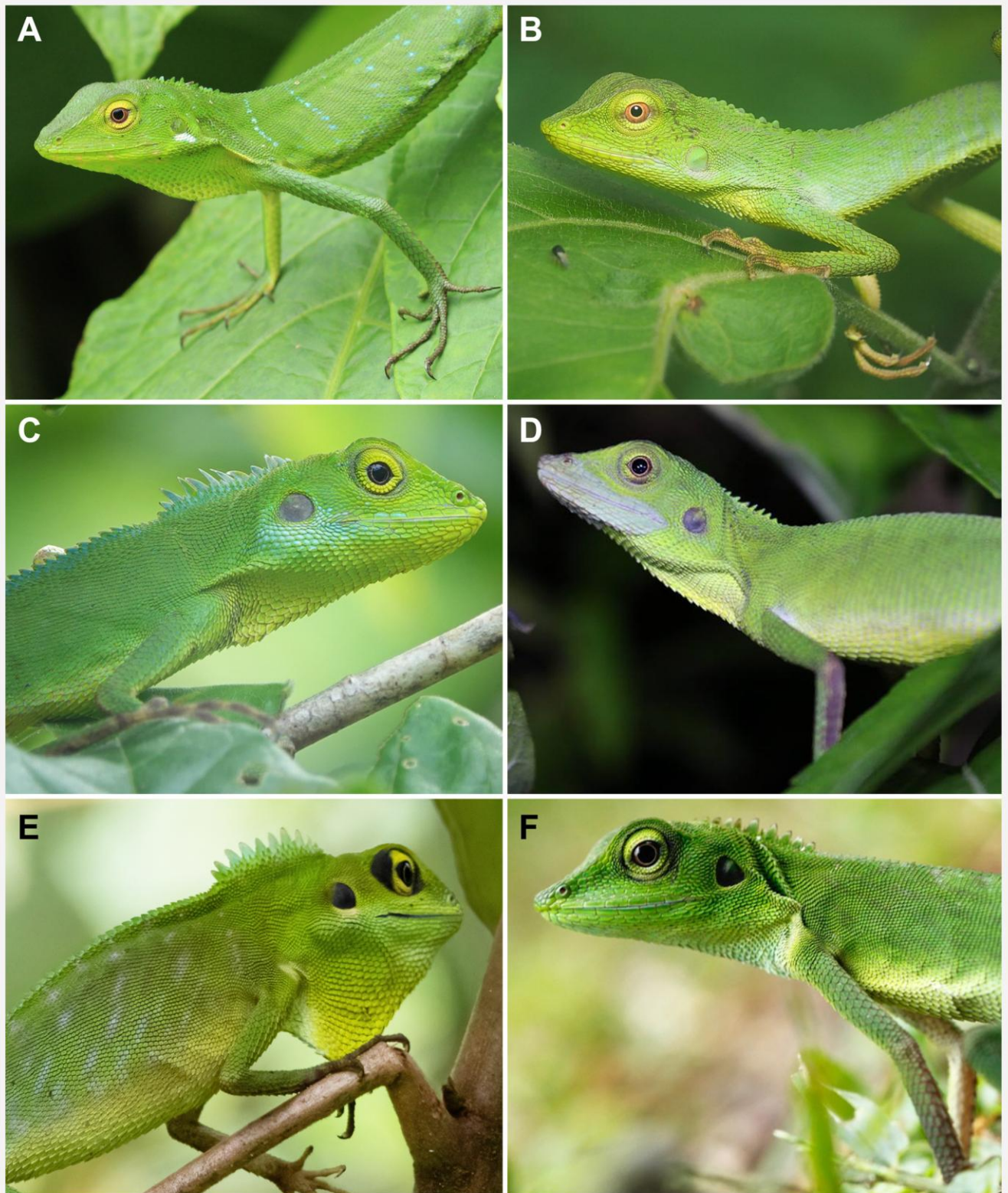


Figure 3. (A) Subadult male of *Bronchocela cristatella* sensu stricto from Tasikmalaya, West Java; (B) subadult female of *B. cristatella* from Sleman, Central Java; (C) adult male of *B. cf. moluccana* from Halmahera, North Maluku; (D) adult female of *B. moluccana* from Ambon; (E) adult male of *B. octospinosa* from Bohorok, North Sumatra; and (F) adult female of *B. octospinosa* from Langkat, North Sumatra, Indonesia (not collected); © Photo: (A) R. Beunen, (B) N.U. Dhiya'ulhaq, (C) B. Harris, (D) T. Kirschey, (E) M. Rose, and (F) S. Hazenberg

Table 2. Diagnostic characters separating the species of *Bronchocela* (modified after Amarasinghe *et al.* 2022b): (1) maximum SVL in adults (in mm); (2) gular pouch absent (a), small (s), or large (l) in males; (3) mid gular scales not enlarged (n) or enlarged (e) in males; (4) number of enlarged ventral scale rows; (5) ventrals $\times$ times larger than dorsals; (6) number of ventrals; (7) lateral body scales narrowly (n) or broadly (b) acute; (8) lateral body scales smooth (sm), feebly (fk) or strongly (sk) keeled; (9) number of upwards pointing upper dorsal scale rows; (10) nuchal crest weak (w) or moderately developed (d) in males; (11) nuchal crest scales crescent-shaped (c) or lanceolate (l) in males; (12) number of nuchal crest scales to the level of axilla in males; (13) longest nuchal crest scale shorter (s) or longer (l) than vertical orbit diameter in males; (14) dorsal crest indistinct (i) or distinct (d) in males; continued.

<i>Bronchocela</i> Species	(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)	(9)	(10)	(11)	(12)	(13)	(14)
<i>B. burmana</i>	94.0	a	n	?	4–5	?	n	sk	0	w	l	6–10	s	i
<i>B. celebensis</i>	119.0	l	e	10–12	1–2	62–78	b	sk	4–6	d	l	8–10	s	d
<i>B. cristatella</i> sensu stricto	107.2	s	n	10–12	4–5	60–82	n	sk	4–6	w	l	10–12	s	i
<i>B. cyanopalpebra</i>	103.6	s	n	10–12	2	76–85	b	fk	3, 4	d	c	7–12	s	i
<i>B. danieli</i>	80.0	a	n	10–12	5–8	75–79	n	sk	3, 4	w	l	12–14	s	i
<i>B. hayeki</i>	120.0	l	e	8–10	8–10	50–60	b	sk	5–7	d	c	10–12	l	d
<i>B. jubata</i>	142.0	l	e	10–12	1	56–73	b	sk	1, 2	d	c	10–12	l	d
<i>B. marmorata</i> sensu lato	123.6	s	n	10–12	1–5	72–74	b	fk	1, 2	w	l	7–13	s	d
<i>B. moluccana</i>	101.5	l	e	8–10	3–5	66–82	n	fk	4, 5	d	c	10–14	s	d
<i>B. nicobarica</i>	79.0	l	n	8–10	1–2	76–80	n	fk	3, 4	w	l	10–12	s	i
<i>B. octospinosa</i>	111.2	l	e	12–14	3–5	60–77	b	fk	8–10	d	c	8–12	s	d
<i>B. orlovi</i>	109.6	s	n	?	2–3	?	b	fk	0	d	c	8–10	l	d
<i>B. petersidoriai</i>	80.0	s	e	8	5–8	82	n	sk	4–6	d	l	12	s	i
<i>B. rubrigularis</i>	106.4	s	e	10–12	2–3	54–72	b	sk	1–2	d	c	8–10	l	d
<i>B. shenlong</i>	106.0	l	e	?	3–5	?	n	sk	4–7	d	l	10–12	s	i
<i>B. smaragdina</i>	113.0	a	e	10–12	4–5	64–72	b	fk	1, 2	w	l	10–12	l	i
<i>B. vietnamensis</i>	122.0	s	e	12	2–3	70–73	b	fk	0	w	l	10–12	l	i

Table 2 (continued). (15) Gap between nuchal and dorsal crests: present (p), absent (a), or not applicable for indistinct dorsal crests (NA); (16) enlarged scales on temporal region: present (p) or absent (a); (17) number of temporal scale rows between the orbit and the tympanum; (18) number of canthal scales between the supranasal and the anterior border of the orbit; (19) canthal edges blunt (b) or sharp (s); (20) number of midbody scale rows; (21) 3rd finger shorter (s) or longer (l) than 4th finger, or equal (e); (22) White transverse markings on body: present (p) or absent (a); (23) number of paravertebrals; (24) number of enlarged paravertebral scale rows at the anterior portion of midbody; (25) Source.

<i>Bronchocela</i> Species	(15)	(16)	(17)	(18)	(19)	(20)	(21)	(22)	(23)	(24)	(25)
<i>B. burmana</i>	NA	a	7, 8	5–7	s	55–71	l	a, p	?	?	This study (<i>n</i> = 17); Zug <i>et al.</i> 2017; Grismer <i>et al.</i> 2015
<i>B. celebensis</i>	p	p	7, 8	3, 4	b	50–76	l	a, p	68–82	0	This study (<i>n</i> = 59)
<i>B. cristatella</i> sensu stricto	NA	p	6–8	5–7	s	61–80	e	a, p	94–116	1	This study (<i>n</i> = 83)
<i>B. cyanopalpebra</i>	NA	p	6, 7	4, 5	s	56–78	s	a	?	0	This study (<i>n</i> = 8)
<i>B. danieli</i>	NA	p	7, 8	4, 5	b	65–71	s	a	?	0	This study (<i>n</i> = 2)
<i>B. hayeki</i>	a	a	7, 8	4, 5	s	64–75	l	p	?	1	This study (<i>n</i> = 14)
<i>B. jubata</i>	a	p	6, 7	5, 6	s	33–59	s	p	50–72	1	This study (<i>n</i> = 200)
<i>B. marmorata</i> sensu lato	a	a	8–10	4–6	s	47–73	e, l	a, p	?	?	This study (<i>n</i> = 62)
<i>B. moluccana</i>	p	p	7, 8	5–7	s	50–68	s	a	80–94	1	This study (<i>n</i> = 133)
<i>B. nicobarica</i>	NA	p	4–6	3, 4	s	62–63	s	a	?	0	This study (<i>n</i> = 3)
<i>B. octospinosa</i>	a	a	8–10	5–7	b	54–76	s	p	94–114	1	This study (<i>n</i> = 40)
<i>B. orlovi</i>	a	a	6	3, 4	s	43	?	?	?	?	This study (<i>n</i> = 1)
<i>B. petersidoriai</i>	NA	a	8–10	6	b	?	l	p	?	?	This study (<i>n</i> = 1)
<i>B. rubrigularis</i>	a	p	6, 7	3, 4	b	50–58	l	a	?	1	This study (<i>n</i> = 6)
<i>B. shenlong</i>	NA	p	6, 7	6–11	s	71–92	s	p	?	?	Grismer <i>et al.</i> 2015
<i>B. smaragdina</i>	NA	a	9, 10	4, 5	b	43–53	l	?	?	0	This study (<i>n</i> = 6)
<i>B. vietnamensis</i>	NA	a	12, 13	4, 5	b	47–54	l	?	?	?	This study (<i>n</i> = 2)

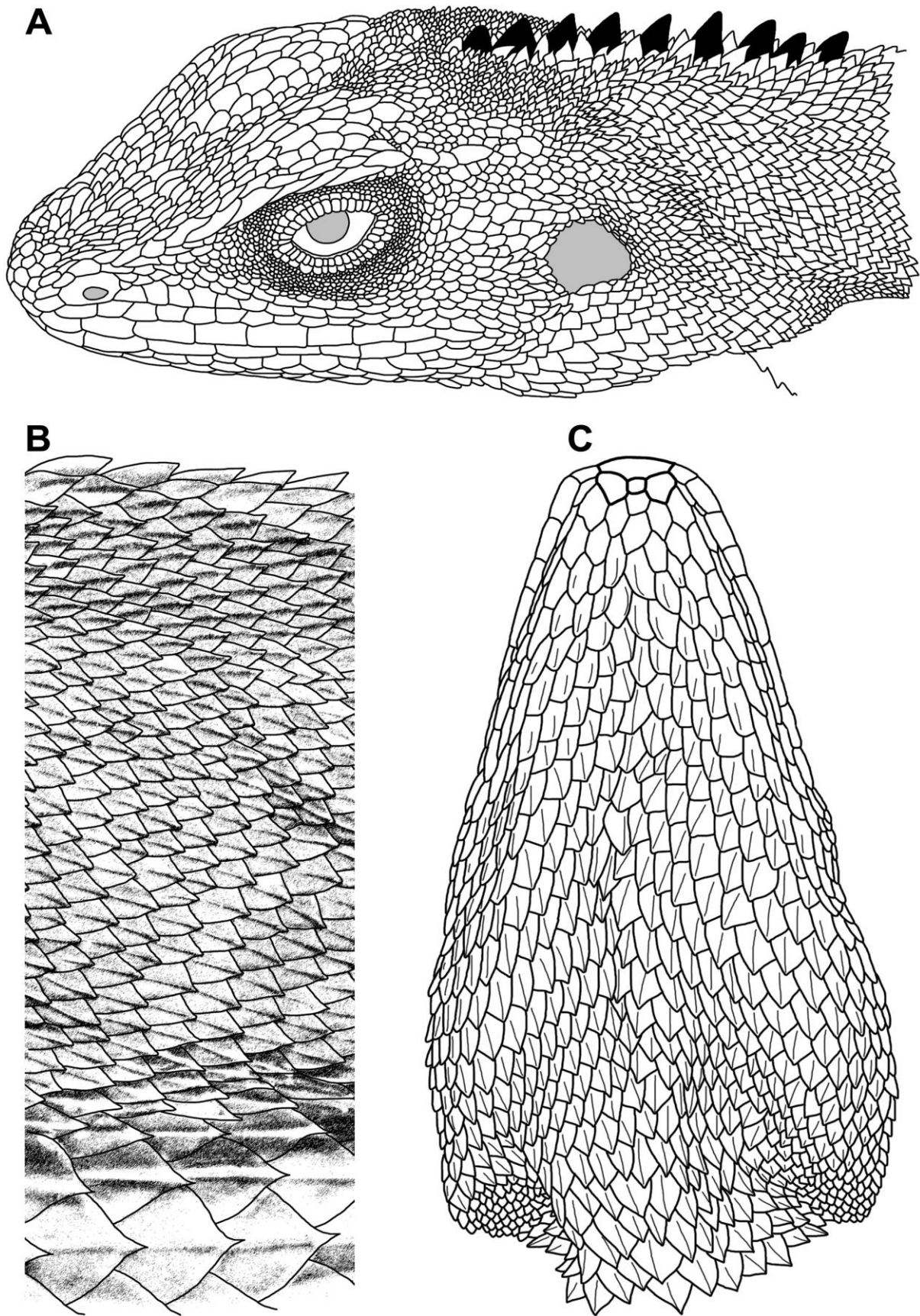


Figure 4. *Bronchocela cristatella* sensu stricto (neotype, male, MZB 6989) from Situ Gede, Tasikmalaya, West Java, Indonesia **(A)** dorsal lateral view of the head (notice the lanceolate and weak nuchal crest), **(B)** lateral body (notice the narrowly acute, strongly keeled scales and directed upward scale rows), and **(C)** ventral view of the head (notice the small gular pouch with non-enlarged midgulars; © Illustrated by A.A.T. Amarasinghe

eye–tympanum length 63.4% of eye diameter; ear opening shallow, its greatest diameter horizontally, tympanum smaller than orbit, around 50% of orbit diameter; tympanum surrounded by strongly keeled scales; temporal scales not enlarged, keeled, juxtaposed, 7–8 scale rows between orbit and tympanum; no supratympanic spines; forehead convex; scales on interorbital and supercilium area keeled; scales on snout keeled, larger in size than those of occipital region; a developed lanceolate-shaped nuchal crest consisting of 10–12 scales up to the level of axilla, no distinct dorsal crest middorsally, no crest on the tail; rostral scale small, hexagonal, width greater than its height, ventroposteriorly in contact with first supralabial, bordered posteriorly by five more or less equal-sized postrostral scales; around nostrils on each side two supranasals, two postnasals, two prenasals, and two subnasals, which separate nasal from supralabials; nostrils round, located middle of the undivided nasal plate; canthus rostralis and supraciliary edges sharp; five canthal scales between supranasal and anterior margin of orbit; no distinct parietal plate; mental enlarged, pentagonal, shorter than wide, in contact with two enlarged postmentals posterolaterally and by a smaller scale posteriorly. In contact laterally with the first infralabial; each postmental pair is bordered posteriorly by five smooth scales, including the medial scale, but exclusive of infralabial; chin scales smooth; gular pouch present and small; throat scales and gular scales keeled, mucronate, and imbricate; midgular scales not enlarged; three scale rows separate orbit from supralabials; supralabials ten (seven in midorbit position); infralabials ten, decreasing in size toward corner of mouth; ventral scales on the neck granular and keeled.

Body slender; lateral body scales equal, narrowly acute, strongly keeled and imbricate; scales on lateral body smaller (approximately 1 / 8th of mid ventrals) in size than those of venter at the same level, directed backward and downward; 4–6 upper dorsal scale rows on the dorsal body directed backward and upward along the body; 64 scales around the midbody; pectoral scales and abdominal scales keeled, mucronate, imbricate and keels forming regular and parallel continuous ventral ridges; abdominal scales slightly larger than pectoral scales; 12 scale rows enlarged ventrally, with a clear boundary from the lateral scales; 63 ventrals.

Forelimbs moderately short; an oblique fold present from angle of mouth to insertion of forelimb; dorsal scales on fore- and hind limbs keeled, enlarged, imbricate and mucronate; ventral scales on upper arm and lower arm keeled, imbricate, and mucronate; hind limbs relatively longer than forelimbs; scales on ventral surface of thigh keeled, enlarged, imbricate and mucronate; tibia comparatively shorter than femur (30.3 versus 36.0 mm); keels on tibia forming a series of continuous parallel ridges; digits elongate, slender; relative length of digits (fingers) $3 = 4 > 2 > 5 > 1$; (toes) $4 > 3 > 5 > 2 > 1$; all bearing slightly recurved claws, claws are sharp and elongate; subdigital lamellae entire, bicarinate, and regular, subdigital lamellae on toe IV (left) 33.

Tail elongated and complete, 300 mm. Ventral scales on tail base keeled and imbricate, larger than on dorsal tail; dorsal scales on tail imbricate, keeled, mucronate, and keels forming the continuous parallel ridge.

Colouration. In preservative, the dorsal side of the body is greyish brown, the lateral head lighter; a white spot below the tympanum; the dorsal head has the same colour as the body; orbit, but not the eye, slightly darker than the head or body, tympanum light grey or brown; scattered cream spots on gular; dorsal spines same colour as body, knee, elbow beige; dorsal fingers and toes brown, anterior tail light grey, banded with dark grey, posterior two-thirds of the tail brown-beige; ventral body, limbs, anterior tail, and gular region pale bluish grey; ventral digits light brown-beige.

In life (Figs. 3A–B), dorsal and ventral colouration is bluish green throughout the body, the distal half of the tail brownish; the head yellowish green laterally and ventrally; a white spot below the tympanum; tympanum and orbit pale and uniform green or luminous green; 5 or 6 sky-bluish dotted lines across the body (not always present).

Variation. Populations across Java, southern Sumatra, and southern Kalimantan exhibit geographically structured but shallow variation. Western Javan individuals typically possess 10 nuchal crest scales, whereas eastern Javan and Balinese populations more frequently bear 12. Eastern Javan populations also show slightly enlarged ventrolateral scales, sometimes creating the illusion of >12 enlarged ventral rows when poorly preserved. Southern Sumatran males tend to develop a proportionally smaller gular pouch

than Javan males, though scale morphology remains consistent across the range. Subadult individuals from all localities often show faint pale lateral spotting that disappears in adulthood.

Remarks. *Agama cristatella* was described by Kuhl (1820), who stated that he examined specimens housed in the “Paris Museum” (now MNHN, Paris). Kuhl departed for Java in December 1820 and died there in September 1821; therefore, all specimens he referenced must have been part of the pre-existing MNHN holdings prior to his departure. Duméril & Bibron (1837) and Duméril (1851) later catalogued all MNHN specimens under the name “*Bronchocela cristatella* Kaup,” including material from Penang, Ambon, Buru, Sumatra, and Java. Among these, two specimens collected by Leschenault in Java—MNHN 6885 and MNHN 1999.8146—are the only individuals demonstrably available to Kuhl before 1820 and were part of the original type series and, following the lectotype designation of Figueroa (2021), are paralectotypes. These syntypes matches Kuhl’s (1820) original description and represent the Javan phenotype.

Figueroa (2021), following Brygoo (1988), designated the Seba (1734) illustration (plate 89, fig. 1) as the lectotype. Although the image is stylized and of limited diagnostic value, already described as “imperfect” by Duméril & Bibron (1837), it forms part of the original type series and therefore represents a permissible lectotype under ICZN Article 74. However, because the illustrated specimen is not associated with a traceable population or locality, the lectotype does not stabilize species identity. The extant Leschenault syntypes, though preferable as lectotype candidates, cannot replace the designated lectotype because Figueroa’s action is nomenclaturally valid.

Given (1) the heterogeneous usage of *B. cristatella* through two centuries, (2) the inadequacy of the iconotype for modern diagnosis, and (3) the impossibility of identifying a complete syntype series, designation of a neotype is required under ICZN Article 75.3 to stabilize application of the name. The neotype chosen here (MZB 6989) originates from Java, the only plausible type locality, and matches both the original description and the Leschenault paralectotypes in all meristic and morphometric traits. It anchors *B. cristatella* sensu stricto to the Javan–southern Sumatran–southern Kalimantan lineage, eliminating more than 180 years of

taxonomic ambiguity surrounding this historically problematic species.

Distribution. Fig. 5. A species of *Bronchocela* inhabiting Java, South Sumatra and Lampung, South and East Kalimantan, and Bali.

Bronchocela moluccana (Lesson, 1830) comb. nov.
(Tables 2, 3; Figs. 3C–D)

Agama moluccana Lesson, 1830:34.

Calotes cristatellus moluccanus — Kopstein 1926;
Brongersma 1933:489; Brongersma 1948:489.

Holotype (by monotypy). An adult specimen of 81 mm SVL (probably a female due to rudimentary nuchal scales in figure 1 on Plate 1 of Lesson 1830) from “Cajéli,” Buru Island, collected by R.P. Lesson between 23rd September and 1st October 1823 and presented to the Paris Museum in 1828, and lost ever since (Brygoo 1988).

Neotype (designated herein). NHMUK 1910.4.26.21, adult male, from Kayeli (= Cajéli), Buru Island, Maluku, Indonesia, collected by G. William Stalker, and entered into the museum registry on 26th April 1910.

Diagnosis. A species of *Bronchocela*, morphologically somewhat close to its allopatric congeners: *B. jubata* on Java, *B. celebensis* on Sulawesi, and *B. hayeki* in Sumatra in body posture and colouration, but differs from all species by having medium-sized body (67.2–101.5 mm SVL; 88.9 ± 9.1 , $n = 19$) in adults; relative tail length (267.8–394.9% of SVL; 321.5 ± 31.2 , $n = 19$); a large gular pouch in males; midgular scales enlarged; 8–10 enlarged ventral scale rows; ventrals 3–5 times larger than dorsals; 66–82 ventrals (73.8 ± 4.7 , $n = 19$); lateral body scales narrowly acute, feebly keeled; 4 or 5 upper dorsal scale rows on the lateral body directed upward along the body; nuchal crest developed, crescent in shape; 10–14 nuchal crest scales to the level of axilla; longest nuchal crest scale shorter than eye diameter; dorsal crest distinct, continue with a 4–6 vertebral scales gap after nuchal crest; scales on temporal region not enlarged; 7 or 8 temporal scale rows between orbit and tympanum; 5–7 canthal scales between supranasal and anterior border of orbit; canthal edge sharp; 50–68 scale rows at midbody (58.6 ± 5.1 , $n = 19$); 3rd finger shorter than 4th finger; 80–94 paravertebrals (86.3 ± 4.2 , $n = 19$), first paravertebral row enlarged.

Comparison. *Bronchocela moluccana* is most likely to be confused with *B. jubata*, the geographically nearest widespread species, especially in Maluku material, where colour polymorphism is misleading. Unlike *B. jubata* (characters in parentheses), *B. moluccana* has 50–68 midbody scale rows (vs. 33–59), feebly keeled lateral scales (vs. strongly keeled), 4–5 upward-directed upper dorsal rows (vs. 1–2), and a continuous dorsal crest behind the nuchal crest separated by a 4–6 scale gap (vs. a dorsal crest merging directly or weakly produced). The gular pouch in males is large (vs. extremely large in *B. jubata*), and the longest nuchal crest scale is shorter than orbit diameter (vs. longer). Within the *cristatella* complex, *B. moluccana* is most similar to *B. cristatella* but differs reliably by having a large gular pouch (vs. small), enlarged midgular scales (vs. not enlarged), feebly keeled lateral scales (vs. strongly keeled), a distinct dorsal crest (vs. indistinct), and fewer midbody scale rows (50–68 vs. 61–80). It is also similar to *B. petersidoriai*, but differs by its feebly keeled lateral scales (vs. strongly keeled) and a dorsal crest distinctly present (vs. indistinct).

Description of the neotype. An adult male, SVL 101.8 mm. Head moderately large, elongate, head length 32.7% of SVL, subtriangular in dorsal and ventral aspects, head width 49.9% of head length; distinct from neck; snout elongate, snout length considerably greater than eye diameter, eye diameter 54.5% of snout length; interorbital distance broad; eye large, pupil rounded; diameter of eyes slightly greater than eye–tympa-num distance, eye–tympa-num length 90.9% of eye diameter; ear opening shallow, its greatest diameter horizontally, tympanum smaller than orbit, around 50% of orbit diameter; tympanum surrounded by strongly keeled scales; temporal scales not enlarged, keeled, juxtaposed, 7–9 scale rows between orbit and tympanum; no supratympanic spines; forehead concave; scales on interorbital and supercilium area keeled; scales on snout keeled, smaller in size than those of occipital region; a developed crescent shaped nuchal crest consisting of 8–10 scales up to level of axilla, with a 4–6 vertebral scales gap, continue as a dorsal crest decreasing in size middorsally, no crest on the tail; rostral scale small, hexagonal width greater than its height, ventroposteriorly in contact with first supralabial, bordered posteriorly by six more or less equal-sized postrostral scales; around nostrils on each side three supranasals, two postnasals, a single

prenasal, and two subnasals, which separate nasal from supralabials; nostrils round, located middle of undivided nasal plate; canthus rostralis and supraciliary edges sharp; five canthal scales between supranasal and anterior margin of orbit; no distinct parietal plate; mental enlarged, pentagonal, shorter than wide, in contact with two enlarged postmentals posterolaterally and by a smaller scale posteriorly; in contact laterally with first infralabial; each postmental pair bordered posteriorly by five smooth scales, including medial scale, but exclusive of infralabial; chin scales smooth; gular pouch present and large; throat scales and gular scales slightly keeled, mucronate, and imbricate; mid gular scales enlarged and strongly keeled; five scale rows separate orbit from supralabials; supralabials ten (seven in midorbit position); infralabials nine, decreasing in size toward corner of mouth; ventral scales on neck keeled.

Body slender; lateral body scales equal, narrowly acute, feebly keeled and imbricate; scales on lateral body smaller (approximately 1 / 5th of mid ventrals) in size than those of venter at the same level, directed backward and downward; 4–6 upper dorsal scale rows on the dorsal body directed backward and upward along the body; 58 scales around midbody; pectoral scales and abdominal scales keeled, mucronate, imbricate and keels forming regular and parallel continuous ventral ridges; abdominal scales larger than pectoral scales; eight scale rows enlarged ventrally, with a clear boundary from the lateral scales; 81 ventrals.

Forelimbs moderately short; an oblique fold present from angle of mouth to insertion of forelimb; dorsal scales on fore- and hind limbs keeled, enlarged, imbricate and mucronate; ventral scales on upper arm and lower arm keeled, imbricate, and mucronate; hind limbs relatively longer than forelimbs; scales on ventral surface of thigh keeled, enlarged, imbricate and mucronate; tibia comparatively shorter than femur; keels on tibia forming a series of continuous parallel ridges; digits elongate, slender; relative length of digits (fingers) $4 > 3 > 2 > 5 > 1$; (toes) $4 > 3 > 5 > 2 > 1$; all bearing slightly recurved claws, claws are sharp and elongate; subdigital lamellae entire, bicarinate, and regular, 36 subdigital lamellae on toe IV.

Tail elongated and broken (191 mm). Ventral scales on the tail base keeled and imbricate, larger than on the dorsal tail in size; dorsal scales on the tail imbricate, keeled, mucronate, and keels forming continuous parallel ridges

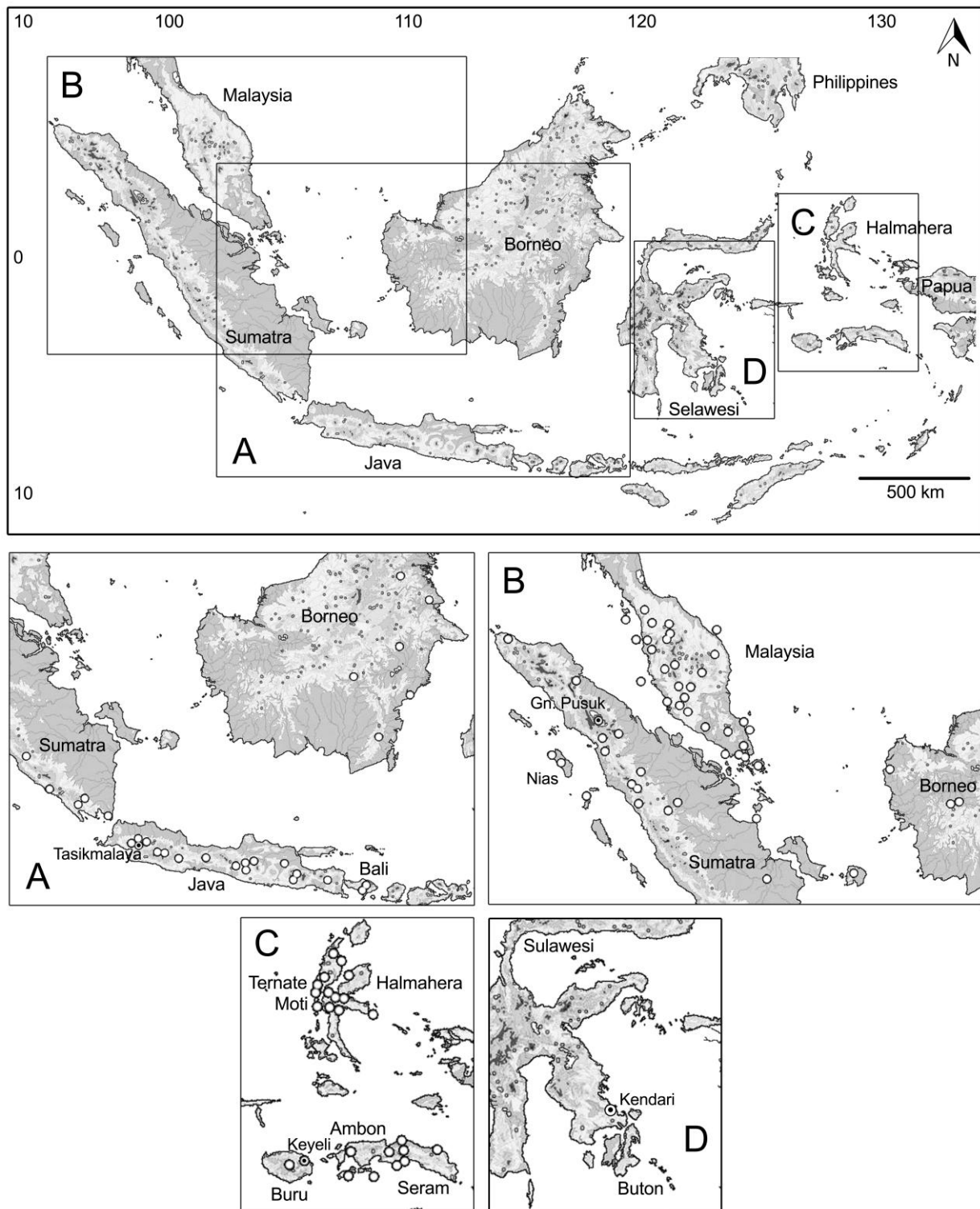


Figure 5. Current distribution of (A) *Bronchocela cristatella*, (B) *B. octospinosa*, (C) *B. moluccana*, and (D) *B. petersidoriai*. Symbols with central dots indicate type localities of the respective species.

Colouration. In the preservative, the dorsal side of the body is olive grey, lateral head is light brownish; dorsal head same colour as the body, except the snout pale brown; orbit, not the eye a little paler than head or body, tympanum light grey or brown; dorsal spines blue; dorsal fingers and toes brownish, anterior tail greyish, not

banded, posterior two-thirds of the tail brownish; ventral body, limbs, anterior tail brown, ventral head and pectoral region pale brown; ventral digits reddish brown.

In life (Figs. 3C–D), dorsal and ventral colouration is bluish green throughout the body, the distal half of the tail brown; the head yellow

ventrally; forelimbs sky blue; no white spot below the tympanum; no markings on the body.

Variation. Specimens from Buru Island (sensu stricto) are relatively uniform, but material from Ambon and Seram shows modest expansion in character states (e.g., crest count, gular pouch size), but remains morphologically congruent with Buru individuals. Buru individuals generally possess 10–12 nuchal crest scales, while some Ambon and Seram specimens reach 14. The gular pouch in males varies in depth, more pronounced in Ambon populations. Ventral scale counts across the Moluccan arc span 66–82, with Seram individuals tending toward higher counts. Although colouration in life is broadly consistent (blue-green dorsum, yellow-green head, brownish distal tail), Ambon specimens occasionally display faint pale lateral marbling absent in Buru material.

In contrast, populations from Halmahera differ consistently in several head and limb proportions, scale row counts, and crest development. Because no multilocus dataset currently exists to evaluate these divergences, Halmahera is conservatively treated as *B. cf. moluccana* pending genomic analysis.

Remarks. *Agama moluccana* was described from “Cajéli” (Kayeli) on Buru Island, based on material Lesson collected during the voyage of La Coquille (1822–1825). The original holotype (by monotypy) has long been considered lost (Brygoo 1988). There are no specimens at MNHN/RMNH that match Lesson’s description or figure with sufficient accuracy, and several specimens historically associated with “*moluccana*” in MNHN are now known to have been collected later by Quoy and Gaimard during the Astrolabe expedition (1826–1829), placing them outside Lesson’s type series. The absence of a preserved holotype, coupled with broad morphological variation across the central Maluku region, has caused persistent instability in the application of the name *moluccana*.

The Lesson’s figure depicts a medium-sized agamid (~81 mm SVL) with lanceolate head scales, feebly keeled lateral scales, and a modest dorsal crest, but lacks diagnostic detail needed to anchor the taxon to any extant population. Biographical accounts of Lesson’s natural history work offer further background (Rallet 1953, Lescure 2015). Because the original type is lost and the figure is insufficient as a modern reference, Article 75 of the ICZN requires designation of a neotype to stabilize usage. The neotype selected here, NHMUK 1910.4.26.21, is

an adult male originating unequivocally from Buru Island, the type locality of *Agama moluccana*.

The specimen was collected by Georg William Stalker (1879–1910), a New Zealand naturalist who collected extensively for the British Museum (Natural History) while prospecting for gold on the Mambare River, New Guinea, beginning in 1905 (Bak 2013). Stalker drowned on 9 January 1910 during the British Ornithologists’ Union Expedition to Central New Guinea (Moore 2004). His final collection (catalogued on 26 April 1910) was returned posthumously to the British Museum (now NHMUK). NHMUK 1910.4.26.21 was part of this shipment and almost certainly collected by Stalker during his last field activities (1905–1910). The specimen matches Lesson’s original description in all major characters, including body size, lanceolate and crescent-shaped crest scales, feebly keeled lateral scalation, and moderate dorsal crest development. The designation of NHMUK 1910.4.26.21 as neotype thus fixes *moluccana* to the Buru population and stabilizes the nomenclature within the central Maluku region.

Distribution. Fig. 5. Central Maluku: Buru Island, Ambon Island, and Seram Island. Populations from Halmahera and adjacent islands in northern Maluku are provisionally treated as *B. cf. moluccana* pending multilocus data.

Bronchocela octospinosa (Baumann, 1913)
comb. nov.
(Tables 2, 3; Figs. 3E–F)

Calotes octospinosus Baumann, 1913:266.

Lectotype (designated herein). NMBE 10118463, adult male, from Battak Mountains (= Gunung Pusuk Buhit), North Sumatra, Indonesia. Paralectotypes: NMBE 10118464–67.

Diagnosis. A species of *Bronchocela*, morphologically somewhat close to its allopatric congeners: *B. cristatella* on Sumatra and *B. burmana* in the mainland Sundaland, but differs from all species by having medium-sized body (75.9–120.0 mm SVL; 95.6 ± 9.8 , $n = 23$) in adults; relative tail length (330.8–367.6% of SVL; 347.1 ± 10.2 , $n = 23$); a large gular pouch in males; midgular scales enlarged; 12–14 enlarged ventral scale rows; ventrals 3–5 times larger than dorsals; 60–77 ventrals (69.5 ± 4.9 , $n = 23$); lateral body scales broadly acute, feebly keeled; 8–10 upper dorsal scale rows on the

lateral body directed upward along the body; nuchal crest developed, crescent shape; 8–12 nuchal crest scales to the level of axilla; longest nuchal crest scale shorter than eye diameter; dorsal crest distinct; no enlarged scales on temporal region; 8–10 temporal scale rows between orbit and tympanum; 5–7 canthal scales between supranasal and anterior border of orbit; canthal edge blunt; 54–76 scale rows at midbody (64.2 ± 5.7 , $n = 23$); 3rd finger shorter than 4th finger; 94–114 paravertebrals (103.8 ± 5.6 , $n = 23$), first paravertebral row enlarged.

Comparison. *Bronchocela octospinosa* is most likely to be confused with *B. cristatella* in regions where historical misidentifications prevail (Sumatra, Peninsular Malaysia, western Borneo). Unlike *B. cristatella* (characters in parentheses), *B. octospinosa* has crescent-shaped nuchal crest scales (vs. lanceolate), 12–14 enlarged ventral rows (vs. 10–12), broader and feebly keeled lateral scales (vs. narrowly acute and strongly keeled), 8–10 upward-directed dorsolateral scale rows (vs. 4–6), and a fully developed dorsal crest (vs. indistinct). The canthal edge is blunt (vs. sharp), and tail length is proportionally shorter (330–368% vs. up to 390%). *Bronchocela octospinosa* also resembles *B. burmana*, though they are allopatric. It differs by having a well-developed dorsal crest (vs. indistinct), broader lateral scales (vs. narrow), and many more upward-pointing dorsal rows (8–10 vs. 0). Nuchal crest scales are crescent-shaped (vs. lanceolate) and more numerous. Confusion with *B. hayeki* is most likely in older museum specimens from Sumatra, as both species can exhibit crescent-shaped nuchal-crest scales. However, *B. hayeki* typically has a sharp canthal ridge and more enlarged temporal scales, whereas *B. octospinosa* has a blunt canthal ridge and fewer enlarged temporals.

Description of lectotype. An adult male, SVL 120 mm. Head moderately large, elongate, head length 30.0% of SVL, subtriangular in dorsal and ventral aspects, head width 51.4% of head length; distinct from neck; snout elongate, snout length greater than eye diameter, eye diameter 50.6% of snout length; interorbital distance broad; eye large, pupil rounded; diameter of eyes greater than eye-tympanum distance, eye-tympanum length 85.3% of eye diameter; ear opening shallow, its greatest diameter horizontally, tympanum smaller than orbit, 41–46% of eye diameter right and left side respectively; tympanum surrounded by weakly keeled scales; temporal scales not enlarged,

keeled, juxtaposed, 8–9 scale rows between orbit and tympanum; no supratympanic spines; forehead convex; scales on interorbital and supercilium area keeled; scales on snout keeled, larger in size than those of occipital region; a developed crescent shaped nuchal crest consisting of 8 spines up to the level of axilla, nearly as long as eye diameter surrounded by small erect scales, continue as a dorsal crest decreasing in size middorsally, a dorsal crest distinct anteriorly and decreasing on hind part of body and on the tail; rostral scale small, hexagonal width greater than its height, ventroposteriorly in contact with first supralabial, bordered posteriorly by five more or less equal-sized postrostral scales; around nostrils on each side two supranasals, two or three postnasals, two prenasals, and two subnasals, which separate nasal from supralabials; nostrils round, located middle of the undivided nasal plate; canthus rostralis blunt and supraciliary edges sharp; five canthal scales between supranasal and anterior margin of orbit; no distinct parietal plate; mental enlarged, pentagonal, shorter than wide, in contact with two enlarged postmentals posterolaterally and by a smaller scale posteriorly. In contact laterally with the first infralabial; each postmental pair is bordered posteriorly by three smooth scales, including the medial scale, but exclusive of the infralabial; chin scales smooth; gular pouch present and large; throat scales and midgular scales keeled, mucronate, and imbricate; midgular scales enlarged; three scale rows separate orbit from supralabials; supralabials ten (eight in midorbit position); infralabials eight, decreasing in size toward corner of mouth; ventral scales on the neck granular and keeled.

Body slender; lateral body scales equal, broadly acute, feebly keeled and imbricate; scales on lateral body smaller (approximately 1 / 6th of mid ventrals) in size than those of venter at the same level, directed backward and downward; 8–10 upper dorsal scale rows on the dorsal body directed backward and upward along the body; 72 scales around the midbody; pectoral scales and abdominal scales keeled, acuminate, imbricate and keels forming regular and parallel continuous ventral ridges; abdominal scales slightly larger than pectoral scales; 14 scale rows enlarged ventrally, with a clear boundary from the lateral scales; 68 ventrals.

Forelimbs moderately short; an oblique fold present from the angle of mouth to insertion of forelimb; dorsal scales on fore- and hind limbs

keeled, enlarged, imbricate and mucronate; ventral scales on the upper arm and lower arm keeled, imbricate, and mucronate; hind limbs relatively longer than forelimbs; scales on the ventral surface of thigh keeled, enlarged, imbricate and mucronate; tibia comparatively shorter than femur (30.3 versus 36.0 mm); keels on tibia forming a series of continuous parallel ridges; digits elongate, slender; relative length of digits (fingers) $4 > 3 > 2 > 5 > 1$; (toes) $4 > 3 > 5 > 2 > 1$; all bearing slightly recurved claws, claws are sharp and elongate; subdigital lamellae entire, bicarinate, and regular, subdigital lamellae on finger III 28 on toe IV 31 (left).

Tail elongate and complete, 430 mm. Ventral scales on the tail base are keeled and imbricate, larger than on the dorsal tail; dorsal scales on the tail imbricate, keeled, mucronate, and keel forming a continuous parallel ridge.

Colouration. In preservative, the dorsal side of the body is greyish blue, lateral head is lighter. A thin light stripe extending from angle of mouth to below anterior tympanum continuing anteriorly as a faded light stripe on the lower lip to the second infralabial, the dorsal head same colour as the body; orbit, but not the eye, slightly darker than head or body, tympanum light grey or brown; dorsal spines same colour as the body, knee, elbow beige; dorsal fingers and toes brown, anterior tail light grey, banded with dark grey, posterior two-thirds of the tail brown-beige; ventral body, limbs, anterior tail, and gular region pale bluish grey; ventral digits light brown-beige. Freshly dead (after Baumann 1913), body colouration green to olive green; the first part of the tail dark banded and the upper hind limb dark banded.

In life (Figs. 3E–F), dorsal and lateral colouration is yellowish green throughout the body, the ventral part of the body yellow; the head yellowish ventrally; forelimbs green; white spot below the tympanum; pale markings on the lateral body.

Variations. Populations across northern Sumatra and western Borneo reveal minor but stable morphological gradients. Sumatra individuals typically have 8–10 nuchal crest spines, whereas Bornean specimens sometimes reach 12. Ventral counts vary from 60–77, with the upper range more frequent in Bornean samples. Juveniles across the range exhibit a characteristic darkened snout, dusky lips, and mottled temporal patches; a dark pectoral ring is present in juvenile males but fades rapidly with growth. Adults from higher elevations (e.g.,

Bohorok, Pusuk Buhit) tend to show stronger development of the dorsal crest and more sharply defined pale lateral blotches. Tail banding is prominent in freshly preserved juveniles but becomes increasingly obscure in large adults.

Remarks. Baumann (1913) described *Calotes octospinosus* based on five specimens from the “Batak Mountains” of North Sumatra, housed at the Naturhistorisches Museum Bern (NMBE 10118463–67). Only one of these individuals (the specimen illustrated in Baumann’s fig. B) conforms exactly to the diagnostic traits of *B. octospinosa*. Among the remaining syntypes, NMBE 10118466 clearly represents an adult *B. octospinosa*, but the remaining specimens (NMBE 10118464–65, 67) are juveniles that lack several adult diagnostic traits used to separate Sumatran *Bronchocela*; therefore, we do not assign them to species beyond their status as type material, and we exclude them from comparisons.

Because the syntype series includes juvenile specimens that are not diagnosable to species with confidence, and because the illustrated syntype provides an unambiguous anchor to the intended concept of *octospinosus*, we designate NMBE 10118463 as the lectotype under ICZN Article 74.7. The specimen is adult, fully diagnostic, and matches in all respects the illustration Baumann used in the original description. This designation stabilizes usage of the name and clarifies its application to the northern Sumatran–Peninsular Malaysian–western Bornean lineage of *Bronchocela*. The remaining syntypes (NMBE 10118464–67) are hereby treated as paralectotypes.

Distribution. Fig. 5. A species of *Bronchocela* inhabiting the northern parts of Sumatra, the western portion of Kalimantan (Borneo), and Peninsular Malaysia. In Peninsular Thailand, this species is expected south of the Isthmus of Kra (approximately south of 10°30'N), but its occurrence there requires confirmation with vouchered material.

Bronchocela petersidoriai Böhme & Bischoff, 1984
(Tables 2, 3)

Bronchocela intermedia Peters & Doria, 1878:375.
Bronchocela petersidoriai Böhme & Bischoff, 1984:151–213 [replacement name for *B. intermedia* Peters & Doria 1878].

Holotype. MSNG 29109, adult male, from Kendari, Southeast Sulawesi, Indonesia.

Diagnosis. A species of *Bronchocela*, morphologically somewhat close to its allopatric congeners: *B. celebensis* on Sulawesi, but differs from all species by having medium-sized body (80.0–100.8 mm SVL) in adults; relative tail length (343.7% of SVL); a small gular pouch in males; midgular scales enlarged; ventrals 8 times larger than dorsals; eight enlarged ventral scale rows; ventrals 80–84; lateral body scales narrowly acute, strongly keeled; 6 upper dorsal scale rows on the lateral body directed upward along the body; nuchal crest developed, lanceolate in shape; 12 nuchal crest scales to the level of axilla; longest nuchal crest scale shorter than eye diameter; dorsal crest indistinct; no enlarged scales on temporal region; 8–10 temporal scale rows between orbit and tympanum; 6 canthal scales between supranasal and anterior border of orbit; canthal edge blunt; 3rd finger longer than 4th finger.

Comparison. *Bronchocela petersidoriai* is most likely to be confused with *B. celebensis*, the syntopic and morphologically nearest species in Sulawesi. Unlike *B. celebensis* (characters in parentheses), *B. petersidoriai* has a small gular pouch in males (vs. large), strongly keeled lateral scales (vs. strongly keeled but with broader scale shape), an indistinct dorsal crest (vs. well-developed), and lanceolate nuchal crest scales 12 in number (vs. 8–10). The canthal edge in *B. petersidoriai* is blunt (vs. sharp). The species also differs in having ventrals 8× larger than dorsals (vs. 1–2× in *B. celebensis*). Within the *cristatella* complex, it may also be confused with *B. moluccana*, but *B. petersidoriai* has strongly keeled lateral scales (vs. feebly keeled), an indistinct dorsal crest (vs. distinct), and fewer enlarged ventral rows (8 vs. 10–12). Its blunt canthal edge (vs. sharp) also distinguishes it.

Description of holotype. An adult male, SVL 80.0 mm. Head moderately large, elongate, head length 36.2% of SVL, subtriangular in dorsal and ventral aspects, head width 46.2% of head length; distinct from neck; snout elongate, snout length slightly greater than eye diameter, eye diameter 91.5% of snout length; interorbital distance broad; eye large, pupil rounded; diameter of eyes greater than eye–tympanum distance, eye–tympanum length 78.1% of eye diameter; ear opening shallow, its greatest diameter horizontally, tympanum smaller than orbit, slightly less than 50% of orbit diameter; tympanum surrounded by feebly keeled scales; temporal scales not enlarged, keeled, juxtaposed, 8–10 scale rows between orbit and tympanum;

no supratympanic spines; forehead convex; scales on interorbital and supercilium area keeled; scales on snout keeled, smaller in size than those of occipital region; a developed lanceolate shaped nuchal crest consisting of 12 scales up to the level of axilla, no distinct dorsal crest middorsally, no crest on the tail; rostral scale small, hexagonal width greater than its height, ventroposteriorly in contact with first supralabial, bordered posteriorly by six more or less equal-sized postrostral scales; around nostrils on each side three supranasals, two postnasals, a prenasal, and a subnasal, which separate nasal from supralabials; nostrils oval located anteriorly of the undivided nasal plate; canthus rostralis blunt and supraciliary edges sharp; six canthal scales between supranasal and anterior margin of orbit; no distinct parietal plate; mental enlarged, pentagonal, shorter than wide, in contact with enlarged postmentals posterolaterally; in contact laterally with the first infralabial; chin scales smooth; gular pouch present and small; throat scales and gular scales slightly keeled, mucronate, and imbricate; mid gular scales enlarged and strongly keeled; four scale rows separate orbit from supralabials; supralabials eleven (eight in midorbit position); infralabials ten, decreasing in size toward corner of mouth; ventral scales on the neck keeled.

Body slender; lateral body scales equal, narrowly acute, strongly keeled and imbricate; scales on lateral body smaller (approximately 1 / 8th of mid ventrals) in size than those of venter at the same level, directed backward and downward; 6 upper dorsal scale rows on the dorsal body directed backward and upward along the body; pectoral scales and abdominal scales keeled, mucronate, imbricate and keels forming regular and parallel continuous ventral ridges; abdominal scales larger than pectoral scales; eight scale rows enlarged ventrally, with a clear boundary from the lateral scales; 82 ventrals.

Forelimbs moderately short; an oblique fold present from angle of mouth to insertion of forelimb; dorsal scales on fore- and hind limbs keeled, enlarged, imbricate and mucronate; ventral scales on upper arm and lower arm keeled, imbricate, and mucronate; hind limbs relatively longer than forelimbs; scales on ventral surface of thigh keeled, enlarged, imbricate and mucronate; tibia comparatively shorter than femur; keels on tibia forming a series of continuous parallel ridges; digits elongate, slender; relative length of digits (fingers) 3 > 4 > 2 > 5 > 1; (toes) 4 > 3 > 5 > 2 > 1; all bearing

slightly recurved claws, claws are sharp and elongate; subdigital lamellae entire, bicarinate, and regular, 36 subdigital lamellae on toe IV.

Tail elongated and complete (275 mm). Ventral scales on the tail base keeled and imbricate, larger than on the dorsal tail in size; dorsal scales on the tail imbricate, keeled, mucronate, and keels form continuous parallel ridges.

Colouration. In the preservative, the dorsal side of the body is olive grey, lateral head is light brownish; dorsal head same colour as the body, except the snout dark brown; orbit, not the eye, a little darker than head or body, tympanum dark brown; nuchal spines cream; around 10 cream transverse bands on the body; dorsal fingers and toes brownish, anterior tail brownish, banded, posterior two-thirds of the tail greyish; ventral body, limbs, anterior tail grey, ventral head and pectoral region cream; ventral digits brown.

Variations. A large female from Buton Island (MZB 4265; SVL 100.8 mm) represents the upper size range currently known for the species, exceeding the holotype male (SVL 80.0 mm). Compared to the holotype, Buton material exhibits proportionally longer heads (head length 30.3 mm) and wider heads (head width 15.7 mm), along with slightly increased snout length (snout length 11.5 mm) and eye diameter (eye diameter 9.0 mm). Limb measurements (e.g., tibia length 27.3 mm; lower arm length 18.5 mm; foot length 35.9 mm) fall within the expected scaling for individuals of similar body size. Midbody and ventral scale counts also vary slightly among localities, with midbody rows typically ranging from 61–76 and ventrals from 80–84. Tail proportions remain consistent across specimens, with relative tail length generally around 330–350% of SVL.

Remarks. *Bronchocela petersidoriai* was introduced by Böhme & Bischoff (1984) as a replacement name (nom. nov.) for *B. intermedia* Peters & Doria, 1878, because *intermedia* was preoccupied in *Calotes*. The holotype (MSNG 29109) derives from Kendari (Southeast Sulawesi) and documents the core diagnostic morphology of the species. Re-examination of historical Sulawesi material and additional specimens from Buton Island and Central Sulawesi confirms that these populations form a cohesive morphological unit.

Distribution. Fig. 5. A species of *Bronchocela* inhabiting Southeast Sulawesi (including the Kendari region), Buton Island, and

Central Sulawesi (based on examined vouchers; see Appendix).

Discussion

Our integrative analyses reveal that populations previously assigned to *Bronchocela cristatella* across the Indonesian Archipelago represent a set of distinct, diagnosable evolutionary lineages rather than a single widespread species. Morphometric, meristic, and qualitative scale characters showed consistent geographic structure, and the mitochondrial 16S phylogeny independently recovered the same sets of populations as well-supported clades. Together, these results provide a coherent taxonomic framework for redefining species limits within the *cristatella* complex in Indonesia.

Morphological structure and sexual dimorphism. Head morphology emerged as the major axis of differentiation across the Indonesian lineages. Traits such as snout length, eye–nostril distance, and head width, along with dorsolateral scale row number and lateral-scale keeling, consistently separated Javan–southern Sumatran–southern Kalimantan specimens (*B. cristatella*), northern Sumatran and western Bornean specimens (*B. octospinosa*), and central Maluku populations (*B. moluccana*). These traits correspond to stable, lineage-specific combinations of crest morphology, ventral scale series, and midbody counts.

Sexual dimorphism across the complex was strong yet consistent in direction: males exhibited larger heads, while females had longer trunks. Similar female-biased trunk elongation related to reproductive allocation has been reported in other oviparous lizards (Vitt & Congdon 1978). Similar patterns have been demonstrated across lizards, where sexual selection and fecundity selection jointly shape head and trunk proportions (Andersson 1994, Fairbairn 1997, Olsson *et al.* 2002).

Functional studies confirm that head dimensions strongly influence bite performance and contest outcomes (Herrel *et al.* 1996, 2001; Verwajen *et al.* 2002). These patterns fit well within general agamid trends, where sexual selection favours cranial hypertrophy in males and fecundity selection favours abdominal volume in females. Importantly, dimorphism did not obscure lineage boundaries; the same characters that differentiated species remained distinct when sexes were analysed separately or together.

Table 3. Lean diagnostic matrix for *B. cristatella*, *B. moluccana*, *B. octospinosa*, and *B. petersidoriai*—summarizing body-scale morphology, morphometrics, and meristics used to separate species.

Species	<i>B. cristatella</i>	<i>B. moluccana</i>	<i>B. octospinosa</i>	<i>B. petersidoriai</i>
Adult SVL max (mm)	107.2	101.5	120.0	80.0
Tail length (% SVL)	278.4–390.0	267.8–394.9	330.8–367.6	343.7
Gular pouch in males	small	large	large	small
Midgular scales in males	not enlarged	enlarged	enlarged	enlarged
Ventral scale rows enlarged (count)	10–12	8–10	12–14	8
Ventrals × larger than dorsals	4–5×	3–5×	3–5×	8×
Lateral body scales – shape	narrowly acute	narrowly acute	broadly acute	narrowly acute
Lateral body scales – keeling	strong	feeble	feeble	strong
Upper dorsal rows pointing upward	4–6	4–5	8–10	4–6
Nuchal crest – development	weak	developed	developed	developed
Nuchal crest – scale shape	lanceolate	crescent	crescent	lanceolate
Nuchal crest scales to axilla	10–12	10–14	8–12	12
Dorsal crest	indistinct	distinct	distinct	indistinct
Nuchal–dorsal crest gap (scales)	NA (no dorsal crest)	present (4–6 vertebral scales)	absent	NA (no dorsal crest)
Temporal scales enlarged	present	absent	absent	absent
Temporal rows (orbit–tympanum)	6–8	7–8	8–10	8–10
Canthal scales	5–7	5–7	5–7	6
Canthal edge	sharp	sharp	blunt	blunt
Finger III vs IV length	equal	3rd shorter than 4th	3rd shorter than 4th	3rd longer than 4th
White transverse body markings	absent/present	absent	present	present (cream bands)
Paravertebrals	94–116	80–94	94–114	—

Integrative species boundaries. Three independent datasets converge on the same species delimitations: (1) Morphometrics: Phenotypes A, B, and C form distinct clusters in principal component analysis space; Univariate tests identify consistent differences in snout and head proportions; (2) Meristics and qualitative morphology: Crest shape, enlarged ventral rows, temporal scale rows, dorsolateral rows, and lateral-scale keeling differ sharply among lineages; These characters remain stable across geography and specimen age; (3) Molecular phylogeny: The 16S phylogeny identifies three major Indonesian clades corresponding exactly to the morphological clusters; Genetic distances among these clades (3.8–6.5%) align with typical interspecific divergences in draconine agamids.

The concordance among datasets supports recognition of four Indonesian species that were historically treated under *B. cristatella*: *B. cristatella* sensu stricto (Java–southern Sumatra–southern Kalimantan), *B. octospinosa* (northern Sumatra–western Borneo–Malay Peninsula), *B. moluccana* (Buru–Ambon–Seram), and *B. petersidoriai* (Southeast and parts of Central Sulawesi). Halmahera specimens are morphologically divergent from central Maluku material and remain provisionally treated as *B.* cf. *moluccana* pending multilocus evidence.

Phylogenetic structure and biogeographic implications. The topology recovered here reflects major biogeographic partitions across Sundaland and Wallacea. Comparable diversification patterns in response to geological and climatic transitions are known from other Southeast Asian reptile radiations (Skipwith *et al.* 2019, Toussaint *et al.* 2021). *Bronchocela cristatella* belongs to a Sundaland-associated lineage distributed across Java and adjacent southern landmasses, which aligns with known connections within the southern Sunda Shelf. These patterns mirror broader biogeographic transitions documented across the Indo-Australian Archipelago (Lohman *et al.* 2011). *Bronchocela octospinosa* occupies the northern Sunda corridor linking northern Sumatra, Peninsular Malaysia, and western Borneo. *Bronchocela moluccana* represents a distinct island-arc lineage restricted to central Maluku, while *B. petersidoriai* corresponds to a Sulawesi-endemic lineage within a broader Wallacean radiation.

Relationships among these regional lineages, however, remain incompletely resolved. Deeper divergences received weak support in both

maximum-likelihood and Bayesian analyses, a predictable limitation of single-locus mitochondrial datasets. Similar deep but weakly resolved phylogenetic splits occur across unrelated Southeast Asian vertebrate lineages (Braun *et al.* 2017). These uncertainties highlight the need for future multilocus or genomic data to clarify historical connections among Sundaland, Sulawesi, and Maluku lineages and to test the monophyly of the morphological complexes recognized here. Genome-scale datasets have proven particularly effective for resolving comparable deep relationships (Lemmon & Lemmon 2013).

Implications for systematics and future research. This revision resolves long-standing taxonomic instability surrounding the use of the name *B. cristatella* by anchoring the species to a neotype from Java and clarifying its diagnostic boundaries. By reinstating *B. moluccana*, *B. octospinosa*, and *B. petersidoriai*, and by documenting their distinctiveness across morphological and genetic datasets, we provide a stable foundation for further research on ecology, biogeography, and conservation across the genus.

Several gaps remain. Halmahera populations require multilocus data to determine whether they represent a distinct species or peripheral divergence of *B. moluccana*. Philippine lineages excluded from this revision represent a separate taxonomic problem that must be addressed independently. Broader genomic sampling across Sulawesi, Maluku, the Nicobar Islands, Vietnam, and Indochina will be necessary to reconstruct deeper evolutionary relationships and fully resolve species complexes within *Bronchocela*. Nonetheless, the present work establishes a robust framework for future comparative studies.

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Author contributions

All the authors contributed equally.

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Supplemental data

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Appendix. Comparative material examined.

- Bronchocela burmana* ($n = 17$). INDONESIA: Sumatra: ZFMK 13352–13368.
- Bronchocela celebensis* sensu lato ($n = 59$). INDONESIA: Sulawesi: NHMUK 1946.8.11.48 (holotype), NHMUK 1871.7.20.166, 1872.4.6.126–127, 1871.7.20.161–165, 1927.4.20.27, 1980.871–872, XXIV.21.i–j; ZMB 688, 8801, 36898; RMNH 3021a–e, 3023a–d, 7419a–e; MZB 189, 3040, 4197, 4265, 5080, 6991–6996, 6998–7006, 7008–7012, 8896–8898; ZSM 365_0.
- Bronchocela cristatella* ($n = 83$). INDONESIA: Jawa: MZB 6989 (neotype), 196, 304, 705, 767, 995, 1668, 3036, 3809, 4895, 7751, 8885–8888, 9649, 9811, 11888, 14124–14125; NHMUK 1885.12.31.15; ZFMK 20783; RMNH 2848a–b; ZMH R00608, 5602–5603, 5623. Kalimantan: MZB 200, 680, 1017, 1640, 3908, 9524, 13249, 13526, 13979; RMNH 7371a–c, 7374a–b; ZMH R04639–R04643, 5586–5591, 5593–5599, 6081–6082; ZMB 51019, 53634; ZFMK 50529–50530. Sumatra: MZB 1569, 1598, 8894, 9802–9805, 9807–9808, 9810, 13407, 13409; ZMB 57217; ZSM 333.1999, 376.1978.d; ZMH R04928.
- Bronchocela cyanopalpebra* ($n = 8$). INDIA: Nicobar Islands: Car Nicobar (DOSMB 5054, holotype; DOSMB 5089, paratype; BNHS 961, 1610, 1662; ZSI 2671, 15033–15034).
- Bronchocela danieli* ($n = 2$). INDIA: Nicobar Islands: Little Nicobar (ZSI 22455, holotype; ZSI 22496).
- Bronchocela hayeki* ($n = 14$). INDONESIA: Sumatra: ZMB 55931 (neotype); MZB 203, 8892–8893, 13839–13840; NHMUK 1889.11.12.12, 1931.11.9.1–2; RMNH 14916; UIMZ 243; ZMH R05470, R05472–R05473.

- Bronchocela jubata* ($n = 200$). INDONESIA: Jawa: MNHN-RA 2542 (lectotype), 1911.0142; MZB 197, 198, 223, 637, 639, 996, 997, 1342, 1462, 1465, 1484, 1649, 1671, 2629, 2916, 2963, 3023–3035, 3037, 3543, 3678, 3733–3734, 3791–3792, 3898, 3911, 4191–4193, 4885–4887, 4896–4899, 5442–5443, 6224–6225, 6639, 6988, 7053, 7057, 7488, 7632, 7754–7755, 7765, 8010, 8013, 8439, 9423, 9787–9789, 9916, 9921, 9925, 10284, 12081–12086, 13194–13195, 13245–13247, 13775, 13898–13900, 13902–13903, 13971, 13973, 14008–14010, 14681–14684, 14687, 14699; NHMUK 1974.3809, 1846.9.11.49, 1851.7.17.69, 1856.11.17.10–1856.11.17.17, 1873.5.3.1–2, 1874.8.14.18–21, 1885.12.31.16, 1896.9.28.1; RMNH 7304, 7417a–b, 35930; TCWC 73121; ZFMK 48897–48906, 48917–48921, 27099–27101; ZMB 14438; ZMH R4934–R4936, 7066–7069, 7070, 7074–7079, 7080–7087; ZMUC R98500; UIMZ 0001–0002. Bali: MZB 4393, 13988. Kalimantan: ZMH R06163. Sumatra: MZB 6612–6616, 6638, 6656–6657, 9757–9758, 9761–9764; RMNH 8646. Unverified locality records: INDIA: Pondicherry (RMNH 3849; MNHN-RA 2543); PHILIPPINES: ZMB 16305; THAILAND: MNHN-RA 1895.0460, ZSM 552, 559; CAMBODIA: RMNH 26743–26744, 26746.
- Bronchocela marmorata* sensu lato ($n = 62$). PHILIPPINES: NHMUK 1946.8.11.16 (holotype), 72.8.20.25–26; RMNH 3022a–d; ZMH R04882; MNHN-RA 5775, 1900.0341, 1999.8131; ZFMK 43702–43713; ZMB 681, 5433, 5642, 49761–49766, 54507; USNM 36167–36168, 58838, 77133–77135, 140839, 318692, 318694–318695, 498716, 498783, 513564–513571, 513836; FMNH 251691; CAS 15457, 20338, 61705, 62398–62399, 131925; ZMUC 148.
- Bronchocela moluccana* ($n = 133$). INDONESIA: Maluku (Buru Island): NHMUK 1910.4.26.21 (neotype), 1910.4.26.22; MZB 1697; ZSM 366 0. Maluku (Ambon, Seram, adjacent islands): MZB 181, 188, 191, 202, 1529, 1681–1682, 1774, 2001, 2322, 6094, 6096–6099, 6100–6105, 6107, 7449–7454, 7631, 7714–7717, 7720–7721, 7984–7988, 8031–8033, 8035–8041, 8237–8244, 8246–8254, 8256–8258, 8900, 8902–8909, 8913–8914, 9909, 13046–13047; NHMUK 1863.2.28.5, 1892.4.13.10, 1913.10.31.7–13, 1971.535, 1998.252; RMNH 3030–3031, 3034a–b, 3035, 3036a–b, 3037a–c; ZMH R04891–R04892, 6083–6084; ZMUC R98502–R98504; ZSM 366a–b, 366_1; UIMZ 0251–0255. Papua: MZB 183, 8806–8810; NHMUK 1870.8.31.135–137; RMNH 3030, 3034A, 3035; ZMH R04927.
- Bronchocela nicobarica* ($n = 3$). INDIA: Nicobar Islands: Little Nicobar (DOSMB 5070, holotype; DOSMB 5055–5056, paratypes).
- Bronchocela octospinosa* ($n = 40$). INDONESIA: Sumatra: NMBE 10118463 (lectotype); MZB 187, 194, 653, 1679, 1872, 1882, 2163, 2379, 4389, 4390, 4594, 4730, 4993, 4995, 5292, 7463–7464, 8895, 9812, 9907, 14732–14734, 15062, 15064; NHMUK 1884.1.8.24–29; ZFMK 60642–60643; ZMH R4893–R4895. Kalimantan: MZB 192, 8890, 13951; NHMUK 1895.5.1.29.
- Bronchocela orlovi* ($n = 1$). VIETNAM: ZISP 22827 (holotype).
- Bronchocela petersidoriai* ($n = 1$). INDONESIA: Sulawesi Tenggara: Kendari (MSNG 29109, holotype).
- Bronchocela rubrigularis* ($n = 6$). INDIA: Nicobar Islands: ZMH R09271 (holotype), R09272 (paratype); DOSMB 5086–5087; BNHS 1609; ZSI 14668.
- Bronchocela smaragdina* ($n = 6$). CAMBODIA: NHMUK 1946.8.11.35–36 (syntypes); FMNH 262309. VIETNAM: USNM 90392, 144202, 146163.
- Bronchocela vietnamensis* ($n = 2$). VIETNAM: FMNH 252295 (holotype); ZISP 22845 (paratype)